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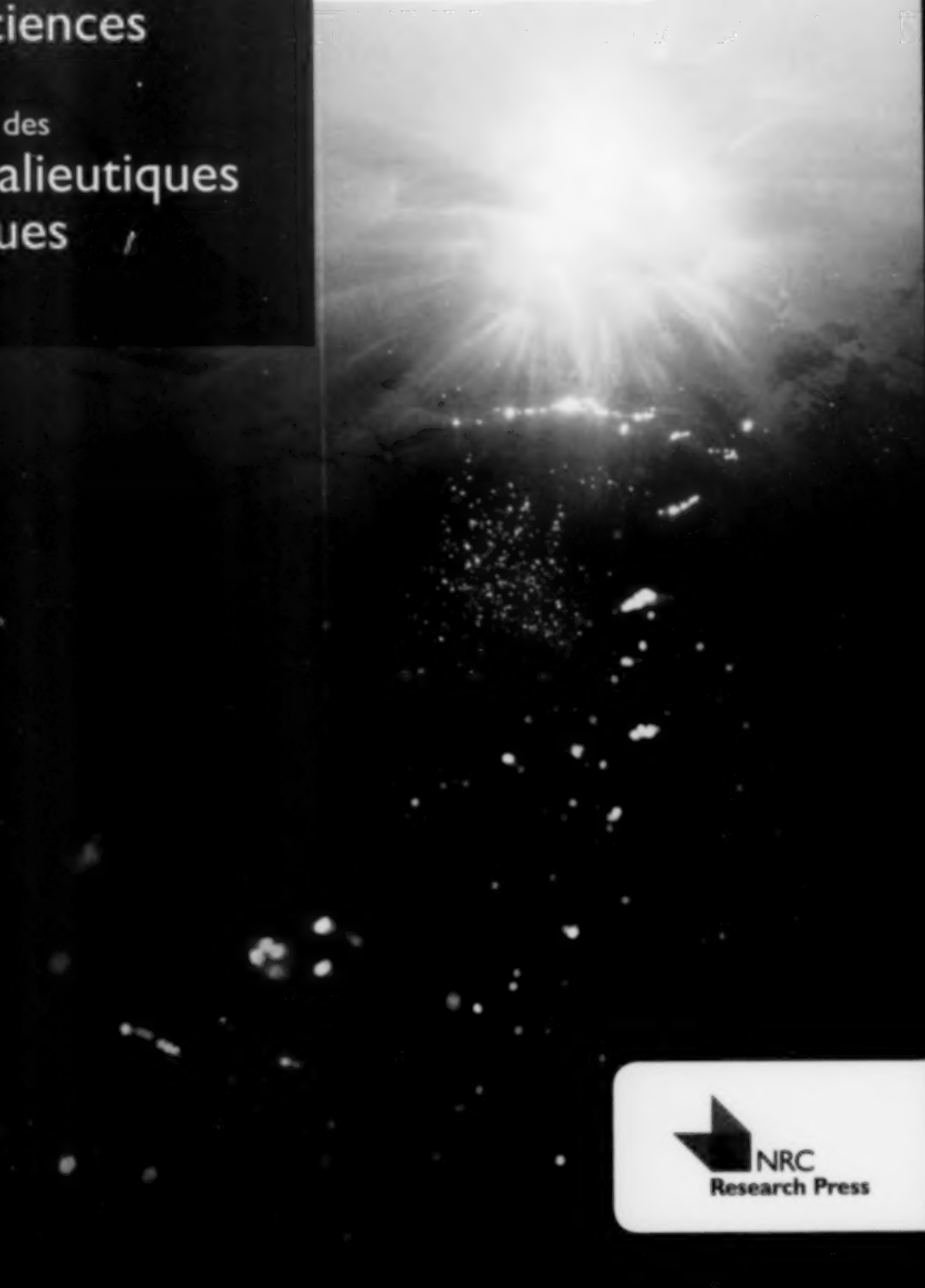

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A whole-lake density reduction to assess compensatory responses of gizzard shad *Dorosoma cepedianum*

Matthew J. Catalano and Micheal S. Allen

Abstract: We used a fishery-induced density reduction of gizzard shad *Dorosoma cepedianum* at a previously unharvested lake to evaluate compensatory density dependence in recruitment processes. We also studied gizzard shad populations at two nearby unharvested lakes to provide contrast with the harvested population. Gizzard shad spawner biomass was reduced by 72% at the harvested lake after 2 years of gill-net removals, although variation in total shad biomass was more modest. We evaluated responses by gizzard shad to the range of biomasses present among the three lakes and 5 years of the study. Annual growth increments varied little over 5 years and were not related to population density across the three lakes. Length-at-maturity differed among lakes and years, but was not related to population density. Despite the range in spawner biomass among the lakes during the study, annual recruitment estimates showed little relationship to the size of the spawner population, suggesting density-dependent prerecruit survival. A spawner–recruit analysis on pooled data from the three lakes indicated that prerecruit survival was negatively related to spawner biomass. Our study provides a rare glimpse of fish compensatory responses following exploitation of a previously unharvested population and has implications for population dynamics theory and fisheries management.

Résumé : Une réduction de densité des aloses à gésier, *Dorosoma cepedianum*, par la pêche dans un lac dans lequel il n'y avait pas eu antérieurement de récolte, nous a servi à évaluer la densité dépendance compensatoire dans les processus de recrutement. Nous avons aussi étudié les populations d'aloses à gésier dans deux lacs adjacents sans récolte afin d'obtenir un contraste avec la population récoltée. La biomasse des reproducteurs chez les aloses à gésier a été réduite de 72 % dans le lac exploité après deux ans de retraits à l'aide de filets maillants, bien que la variation dans la biomasse totale des aloses ait été plus modeste. Nous avons évalué les réactions des aloses à gésier à la gamme de biomasses présente dans les trois lacs et au cours des cinq années de notre étude. Les incréments annuels de croissance ont peu varié au cours des cinq ans et ne sont pas reliés à la densité de population dans les trois lacs. La longueur à la maturité variait en fonction des lacs et des années, mais n'était pas reliée à la densité de population. Malgré l'étendue de la biomasse des reproducteurs dans les lacs durant l'étude, les estimations du recrutement annuel montrent peu de relation avec la taille de la population des reproducteurs, ce qui laisse croire qu'il y a une densité dépendance dans la survie avant le recrutement. Une analyse des reproducteurs-recrues faite sur l'ensemble des données des trois lacs indique que la survie avant le recrutement est en relation négative avec la biomasse des reproducteurs. Notre étude fournit une rare perspective sur les réactions compensatoires des poissons à la suite d'une exploitation d'une population antérieurement inexploitée et elle a des conséquences sur la théorie de la dynamique des populations et la gestion des pêches.

[Traduit par la Rédaction]

Introduction

Compensatory density-dependence is a negative feedback on population growth rate via functional relationships between population density and vital rates. Understanding the strength and forms of compensation is a pervasive theme in natural resource management, because these factors determine the ability of animal populations to withstand anthropogenic perturbations. Density-independent processes are important in determining year-to-year variability in demographic rates of animals, and density-dependence plays a critical role in regulating population size (Murdoch 1994; Brooks and Bradshaw 2006). Without compensation, populations would increase unbounded or be driven to extinction stochastically. However,

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the detection of density dependence in natural populations is challenging (but see Brooks and Bradshaw 2006) owing to inadequate analyses (Rotella et al. 2009), environmental noise, and the difficulty of manipulating animal population density at an appropriate spatial or temporal scale. Compensation occurs through density-dependent changes in rates of survival, reproduction, or migration. Understanding the vital rates and life stages in which density dependence occurs can provide insight into how populations might respond to perturbations such as harvesting or changes in habitat quality and quantity.

There is strong support for the existence of compensatory density dependence in fish populations (Goodyear 1980; Myers et al. 1999; Rose et al. 2001). Recent meta-analyses of spawner–recruit data have confirmed that fish populations exhibit strong compensatory density-dependence via changes in reproduction (Myers et al. 1999; Myers 2001, 2002). Compensation results in high per capita reproductive rates in fishes at low spawner abundance, and relatively low reproductive rates at high abundance (Myers et al. 1999). The strength of density dependence varies widely across species, and likely depends on life history strategy (Winemiller and Rose 1992), habitat structure, and species interactions (Rose and Cowan 2000). Such changes may result from shifts in the availability of food and space, owing to the relaxation of intraspecific competition.

There is evidence that compensation may occur through changes in demographic rates, both during early life (larval and juvenile; i.e., prerecruit phase) and the adult life stage (i.e., postrecruit). Larval and juvenile life stages are particularly important regulators of fish populations (Hjort 1914; reviewed by Heath 1992), and even small changes in demographic rates during these stages can cause substantial change in subsequent adult abundance (Houde 1989). Compensation during the early life phase can occur through changes in growth (Zijlstra and Witte 1984; van der Veer 1986; Peterman and Bradford 1987) or variation in survival related to risk-sensitive foraging behaviors (Walters and Juanes 1993). Density dependence in adult life stages, such as changes in maturation schedules, condition (leading to increased fecundity), egg size and quality, and growth can also regulate population growth (Trippel 1995; Rochet 1998; Rochet 2000).

A central problem in understanding compensation in animal populations is the difficulty in manipulating population densities on an adequate scale to measure density-dependent population responses. Many studies have treated exploited fish populations as replicates from which to draw inferences regarding the strength and mechanisms of density dependence (Rijnsdorp 1993; Myers et al. 1999; Goodwin et al. 2006) . However, these studies rarely include reliable data before fishing, and there are no observations from unmanipulated systems for comparison with harvested populations. Moreover, management practices often aim to maintain exploited populations within bounds to maximize production, which reduces contrast in population density and thus limits the utility of exploited fisheries for evaluating density dependence.

Whole-lake manipulations provide the appropriate scale for detecting meaningful responses (Schindler 1998). Smith and Walters (1981) advocated large-scale adaptive management of ecosystems, whereby individual fish stocks are treated as replicates under varying levels of exploitation, some of which cause population failure. Such studies are rarely feasible, and are politically challenging because of the many individuals who depend on these stocks for their livelihoods (Walters and Martell 2004). Thus, fish density reductions at large spatial scales (i.e., whole lake) are relatively rare in the literature (but see Healey 1978, 1980; DeGisi 1994).

In Florida, USA, the St. Johns River Water Management District (SJRWMD) used a whole-lake density reduction of omnivorous gizzard shad, *Dorosoma cepedianum*, at a eutrophic lake as a restoration tool to reduce phytoplankton abundance and improve water clarity. The removal reduced the total gizzard shad biomass by approximately 30% from 2005 to 2007 (Catalano et al. 2010). The biomass of large (>300 mm) gizzard shad was reduced by 75% over the 2 years because the fishery was selective for larger individuals (Catalano et al. 2010). The removal provided the opportunity to evaluate compensatory responses of the gizzard shad population across a wide range of densities. In this study, we estimated differences in adult growth, maturation, and prerecruit survival of gizzard shad across a range of densities at one harvested and two unharvested lakes.

Materials and methods

Study site

The study was conducted at lakes Dora, Eustis, and Harris, in Lake County, Florida. Lake Dora was the harvested lake where gizzard shad density reduction occurred, and the other lakes were unmanipulated. All lakes were large (>2000 ha), shallow (3 m average depth), eutrophic lakes (mean chlorophyll *a* concentrations > 50 μg·L^{-1}) with similar fish communities. Lake Dora is composed of two distinct basins: Lake Dora, and the smaller Lake Beauclair. The two basins are separated by a 300-m long × 80-m wide canal. Gizzard shad harvest occurred in both basins, so they were treated as one system for these analyses and will be referred to collectively as Lake Dora hereinafter. Narrow canals (<30 m wide, >1.0 km long) also connected Lake Dora to Lake Eustis and Lake Harris to Lake Eustis. The degree to which gizzard shad moved among the lakes was unknown. Preliminary analysis of gizzard shad size and age structure data suggested that the populations were independent to the extent that removals in one lake did not affect the age/size structure in the unharvested lakes (Catalano and Allen 2010).

Removal of gizzard shad at Lake Dora was achieved with a government-subsidized commercial gill net fishery by the SJRWMD. Prior to fish removal, gizzard shad populations at all lakes were unharvested. Gizzard shad were removed from Lake Dora during March–April 2005 and again during January–April 2006. Gizzard shad were removed using gill nets with a minimum mesh size restriction of 102 mm, which selected for gizzard shad larger than approximately 300-mm total length (Catalano et al. 2010). Removal was carried out by an average of five boats setting 3–5 sinking gill nets per day, each net ranging in length from 75 to 600 m.

We evaluated density-dependence in growth, maturity, and prerecruit survival using data from the density reduction at Lake Dora and two unharvested lakes. There are two ways to approach this type of study. One approach would be to conduct a classical before-after-control-impact (BACI) analysis treating each lake as a replicate in an analysis of variance framework. In such designs, unmanipulated systems are treated strictly as a reference system for comparison with the treatment system. However, we were interested in density effects on demographic rates, and density varied at the unharvested lakes as well, although not as much as at Lake Dora. Moreover, applying BACI design in our study system with lake (n = 1 manipulated and n = 2 unmanipulated lakes) as the experimental unit would result in extremely low power to detect effects, owing to the small sample size. Thus we took a regression-type approach and treated density as a continuous variable by including all lake-years as independent observations, which is an assumption common among whole-lake manipulation studies because large numbers of true replicates are not feasible (Carpenter et al. 2001; Vadeboncoeur et al. 2001).

Field data collection

Data regarding the magnitude of the gizzard shad density reduction were collected by SJRWMD from a fishery-dependent onboard observer program. Onboard observers recorded fishery catch-per-effort in 102-mm gill nets and measured a subsample of 100 harvested gizzard shad per week to characterize the length composition of the catch. The cumulative catch and total harvest (kg) each year were tabulated from mandatory trip tickets, which were submitted to the SJRWMD daily by each fisher.

Gizzard shad were collected via annual fishery-independent gill net surveys conducted by the authors (University of Florida, UF) and SJRWMD at each lake. The UF survey set multipanel floating gill nets at 20 fixed randomly-selected sites at each lake in January/February (all lakes, 2005–2009) and November (all lakes, 2004–2006; Lake Dora, 2009). The SJRWMD survey set multipanel gill nets at 10 fixed sites at Lakes Eustis and Harris and 20 sites at Lake Dora during January (Lake Dora, 2003, 2005–2009; Lake Eustis, 2003, 2006–2009; Lake Harris, 2003). Survey gill nets were 2.4-m deep and contained five, 15.3-m long panels of 76, 89, 102, 114, and 127-mm stretch monofilament mesh and nets were set for 2 h each. The UF gill nets had three additional panels of 38, 51, 64-mm mesh to target age-1 fish.

We collected information on size, age, and maturity for gizzard shad. Captured gizzard shad from both surveys were counted and measured for total length (mm). Gizzard shad from the UF survey were aged by analyzing otoliths from a subsample of 10 fish per 10-mm length interval; fish from SJRWMD surveys were not aged. At the lab., fish were measured, weighed, and otoliths were sectioned using a South Bay Tech© Model 650 low-speed saw and aged by three independent readers using a dissecting microscope. The length and age composition of the UF survey data were estimated from the length distribution by multiplying the number of fish captured in each length interval by the proportion of fish at each age within that interval (i.e., age–length key method). Sex was determined on aged fish and the ovaries removed, weighed (g), and preserved in 10% buffered formalin solution to assess age and size at maturity. To verify that the January/February survey was carried out when female gizzard shad were at or near peak spawning condition, additional gill nets (1–3 nets) were set twice per month from January to May 2005–2007 at each lake. At least 30 adult females were collected per trip to assess temporal trends in the gonadosomatic index (GSI; GSI = ovary mass/(fish mass – ovary mass)), which indicated the duration and peak of the spawning period.

Recruitment

Recruitment and other critical demographic parameters were estimated using the data collected above in an age-and-length-structured population model (Catalano and Allen 2010). The model was fitted to gizzard shad data from the three lakes to estimate time-specific annual recruitment to age 1 for lake i ($R_{t,i}$), age and time-invariant instantaneous natural mortality (M_i), von Bertalanffy growth parameters (asymptotic length, $L_{\infty i}$; metabolic parameter, K_i, time-at-zero length, t_{0i}), and gear selectivity parameters (fishery and survey) using a multinomial maximum likelihood function. Data inputs were (*i*) length- and age-specific gill net catches from the November and January/February UF fishery-independent surveys, (*ii*) annual length distributions from the January SJRWMD fishery-independent gill net surveys, (*iii*) gizzard shad length distributions of the 2005 and 2006 Lake Dora harvest from the onboard observers program, and (*iv*) total harvested biomass at Lake Dora in 2005 and 2006. The model was conditioned on total harvested biomass (observed harvest was subtracted from predicted biomass in the model) and likelihood terms for each of the other three data sources were summed to calculate the total likelihood. Parameter uncertainty was evaluated by sampling from the posterior distribution of parameters with Markov Chain Monte Carlo (MCMC) simulation using the Metropolis–Hastings algorithm (Hastings 1970). We simulated 250 000 iterations with a burn-in period of 25 000 and thinning interval of 250. The tuning parameter was set to obtain an acceptance rate of 0.25. Convergence of the chains was evaluated by inspecting trace plots. Sampling from the posterior distribution of the length-age model parameters was used to assess uncertainty in density-dependent parameters of gizzard shad (see Prerecruit Survival, below).

The model scaled the recruitment estimates (i.e., age-1 abundance) at Lake Dora such that they were large enough to explain the observed harvested biomass in 2005 and 2006. Therefore, annual recruitments at Lake Dora could be freely estimated as parameters in the model. However, recruitments at Lakes Eustis and Harris had no scaling information because those lakes were unharvested. Thus, recruitments at Lakes Eustis and Harris were estimated as log-normally distributed residuals ($\omega_{t,i}$) around an average annual recruitment value of 1.0:

$$(1) \qquad R_{t,i} = \overline{R}\exp(\omega_{t,i} - 0.5\sigma^2_{R,i})$$

and the variance was constrained using a penalty function that was added to the total likelihood value:

$$(2) \qquad -\ln P(\omega_{t,i}|\sigma_{R,i}) = \sum_{t} \ln(\sigma_{R,i}) + \frac{\omega^{R}_{t,i}}{2\sigma^2_{R,i}},$$

where $\sigma_{R,i}$ is the standard deviation of the recruitment residuals and is a freely estimated parameter (Maunder and Deriso 2003). This approach maintained an average recruitment of 1.0 and constrained the standard deviation of the recruitment residuals to realistic values at lakes Eustis and Harris.

Growth

We tested for density dependence of fish growth rates by modeling associations between annual growth increments and population biomass across the three lakes. Length and age data from the UF January gill net survey were used to calculate mean length-at-age using methods of DeVries and Frie (1996) for age-length keys. This approach produces unbiased means when aged fish are subsampled on fixed length intervals for an age-length key (i.e., 10 fish per 10-mm length interval). Growth increments were calculated as the difference in mean length from one year to the next for a given cohort and were ln-transformed. Growth increments were obtained for the 2003–2007 cohorts and were limited to age-5 or younger fish because of low sample sizes of older age classes. Analysis of covariance was used to test for effects of total population biomass on logged growth increments using age as the concomitant variable and lake as a block factor in the model. Here we define total biomass as the annual total population biomass at the beginning of the year over which the growth increment was calculated. It was calculated as the predicted numbers of fish in each 10-mm length interval multiplied by the mean weight of fish of that interval using a lake and time invariant length–weight relationship. Biomass estimates were obtained as outputs from the length age model and were rescaled to a mean of zero for each lake. Model selection was carried out using Akaike's information criterion (AIC).

Maturity

We developed a relationship between GSI and maturity using a subset of female gizzard shad. This allowed the use of GSI as a proxy for maturity. Histological sections were prepared from formalin-preserved ovaries from Lakes Dora and Eustis in late January to early March 2007 when fish were in peak spawning condition. Gizzard shad are batch spawners and reproduce over a 2–3 month period in central Florida (M. Catalano, personal observation). Preliminary analyses of temporal trends in GSI from January to May indicated that fish were in peak spawning condition from late-January to early March, and this pattern was relatively consistent across years. Thus only females collected during January–March were used in the analysis to minimize bias due to the timing of sampling relative to spawning. We sampled at least five females per 25-mm length interval. Histological sections were stained with hematoxylin and eosin, embedded in paraffin, sectioned, and mounted on a glass slide at the University of Florida College of Veterinary Medicine, Department of Tissue Pathology. Females were considered mature if histology showed the presence of vitellogenic (yolked) oocytes. Maturity was modeled as a function of GSI using logistic regression and tested for lake and lake × length effects. Probability of maturity was estimated as a function of GSI for females from lakes and (or) years with no histological information. Individuals with a model-predicted probability of maturity exceeding 0.5 were classified as mature and all others were classified as immature.

We modeled maturation as a cohort-specific process, with each cohort potentially maturing according to its own cohort-specific maturation function. We evaluated two types of density effects on cohort maturity: intercohort and intracohort. Intercohort effects were modeled by including a term for the total biomass (B_{2+}) of all other age-classes when a given cohort recruited to age 1. Intracohort effects were modeled by including a term for cohort size, or the total abundance of a cohort. Population biomass estimates were obtained from the length–age model and were rescaled to a mean of zero for each lake, as in the Growth section above. Cohort size was the annual recruitment estimate (numbers of fish) for each cohort from the length–age model and was also rescaled to a mean of zero for each lake. Maturity (probability of maturity) was modeled as a function of length, cohort size, B_{2+}, lake, and lake × length interactions with logistic regression. The lake × length interaction tested whether the shape of the maturity schedule varied among lakes. Preliminary analyses indicated that length was a better predictor of maturity than age, but the two factors were highly collinear. Thus age was excluded from the maturity models. Model selection was carried out using AIC. Associations between cohort size or population biomass and maturity would indicate density dependence in maturation.

Prerecruit survival

Lake- and year-specific prerecruit survival ($S_{t,i}$) was estimated from the length-age model by dividing annual estimates of recruitment ($R_{t,i}$) by the model-predicted total spawner biomass ($B_{t-1,i}$) from the previous year. Spawner biomass was calculated for lake i and time t as:

$$(3)\qquad B_{t-1,i} = \sum_{l}\sum_{a} N_{l,a,t-1,i}\, m_{l,a,t-1,i}\, w_l - H_{t-1},$$

where $N_{l,a,t-1,i}$ is the model-predicted number of age-a gizzard shad of length l in the population at time t, $m_{l,a,t-1,i}$ is the length-, age-, and time-specific proportion of mature fish at lake i, w_l is the mass of a length-l fish, and H_{t-1} represents the spawner biomass that was removed by the fishery just prior to the spawn in the previous year. Population numbers ($N_{l,a,t-1,i}$) were predicted from the model as a function of estimated parameters (Catalano and Allen 2010). Maturity was predicted from the best logistic regression model relating maturity to length, lake, and cohort year (see section on Maturity, above). Fish mass (g) is commonly used as a proxy for fish fecundity (Quinn and Deriso 1999) and was estimated from gizzard shad length data (l) from the lakes using the lake-invariant allometric relationship $w_l = 6.97 \times 10^{-7}\, l^{3.49}$ ($R^2 = 0.99$). Preliminary analyses showed that relative ovary mass (gonadosomatic index) did not vary as a function of population biomass (M.J. Catalano and M.S. Allen, unpublished data). Therefore a constant length–weight relationship was a reasonable approximation for fish mass and ultimately spawner biomass. We did not assess variation in egg size with changes in population density. Thus our estimates of compensatory juvenile survival encompassed changes in survival as well as any unmeasured changes in egg numbers attributable to changes in egg size.

The harvest in 2006 began before gizzard shad spawned, which caused a further reduction in spawner biomass. Examination of the densities of yolked larval gizzard shad from biweekly larval fish tows suggested that approximately half of the catch had been taken before the gizzard shad spawned. Thus we subtracted from the B_t an estimate of the spawner biomass that was removed just prior to the spawn in the previous year:

$$(4)\qquad H_{t-1,i} = 0.5\sum_{l}\sum_{a} N_{l,a,t-1,i}m_{l,a,t-1,i}w_l v_l u_{t-1},$$

where v_l is the length based selectivity of the fishery and u_{t-1} is the proportion of vulnerable sized fish harvested the previous year (exploitation rate).

Annual recruitments were scaled differently at Lake Dora (scaled to the observed harvest) than at Lakes Eustis and Harris (scaled to mean of 1.0 fish). Prerecruit survival was a quotient and was thus dimensionless and comparable among lakes, but spawner biomass was scaled to the annual recruitments and thus was not comparable. Consequently, spawner biomass was rescaled to a mean unfished value of 1.0 kg at each lake prior to use in estimating density dependence in prerecruit survival. The mean unfished spawner biomass at Lake Dora was the average of the 2003 to 2005 predensity reduction estimates.

The strength of density-dependent recruitment at the lakes was evaluated by modeling prerecruit survival as a function of spawner biomass and environmental factors using the linear form of the Ricker stock-recruit function:

$$(5)\qquad \ln(S_{t,i}) = \ln(\alpha) - b_i B_{t,i} + w_t t + \varepsilon_{t,i},$$

where α is the maximum prerecruit survival at very low population density (initial slope of recruitment vs. spawner biomass relationship) and was the parameter of primary interest in this model, b is a population scaling parameter, and the w_t terms represent annual environmental effects on prerecruit survival that act on all of the lakes. Including these shared environmental affects in the model may help ameliorate bias due to serial autocorrelation in prerecruit survival and spawner biomass (Walters and Martell 2004). The mechanism for these environmental effects was not of interest, but visual examination of temporal trends in survival suggested that the lakes were affected by a shared environmental influence on year class strength, which is not uncommon for geographically proximate fish populations (Maceina and Stimpert 1998).

Myers et al. (1999) concluded that the Ricker model was appropriate for evaluating density-dependent recruitment for a range of species when the primary parameter of interest is α. However, the magnitude of α is not comparable among populations unless it is compared to prerecruit survival in an equilibrium unharvested population. Thus, the more valuable measure of density-dependence of prerecruit survival is the maximum lifetime reproductive rate ($\hat{\alpha}$; Myers et al. 1999). This value represents the ratio of prerecruit survival at low population density to survival in the unfished condition and is a standardized measure of density dependence that is comparable across populations (Myers et al. 1999). We calculated $\hat{\alpha}$ for each lake as:

$$(6)\qquad \hat{\alpha}_i = \alpha\phi_{0,i},$$

where $\phi_{0,i}$ is the equilibrium lifetime spawner biomass per recruit for gizzard shad at lake i:

$$(7)\qquad \phi_{0,i} = \sum_{a} s_{a,i}w_a M_{a,i},$$

where $s_{a,i}$ is the survivorship to age a, w_a is the average mass, and $m_{a,i}$ is the proportion mature to age a. Uncertainty in the maximum lifetime reproductive rate was assessed by repeatedly fitting the stock-recruitment model to survival and spawner biomass estimates taken from posterior samples of the parameters obtained via the MCMC simulation of the length–age model.

Observation error in spawner biomass and serial correlation between prerecruit survival and spawner biomass can cause overestimates of α (reviewed by Walters and Martell 2004). Monte Carlo simulation was used to explore these potential biases. We simulated a fish population using length-age model estimates of gizzard shad population parameters, simulated a time series of random recruitments and subsequent spawner biomass assuming a known α, sampled from stock and recruit pairs with observation error, fit the Ricker model and evaluated bias in α estimates.

Results

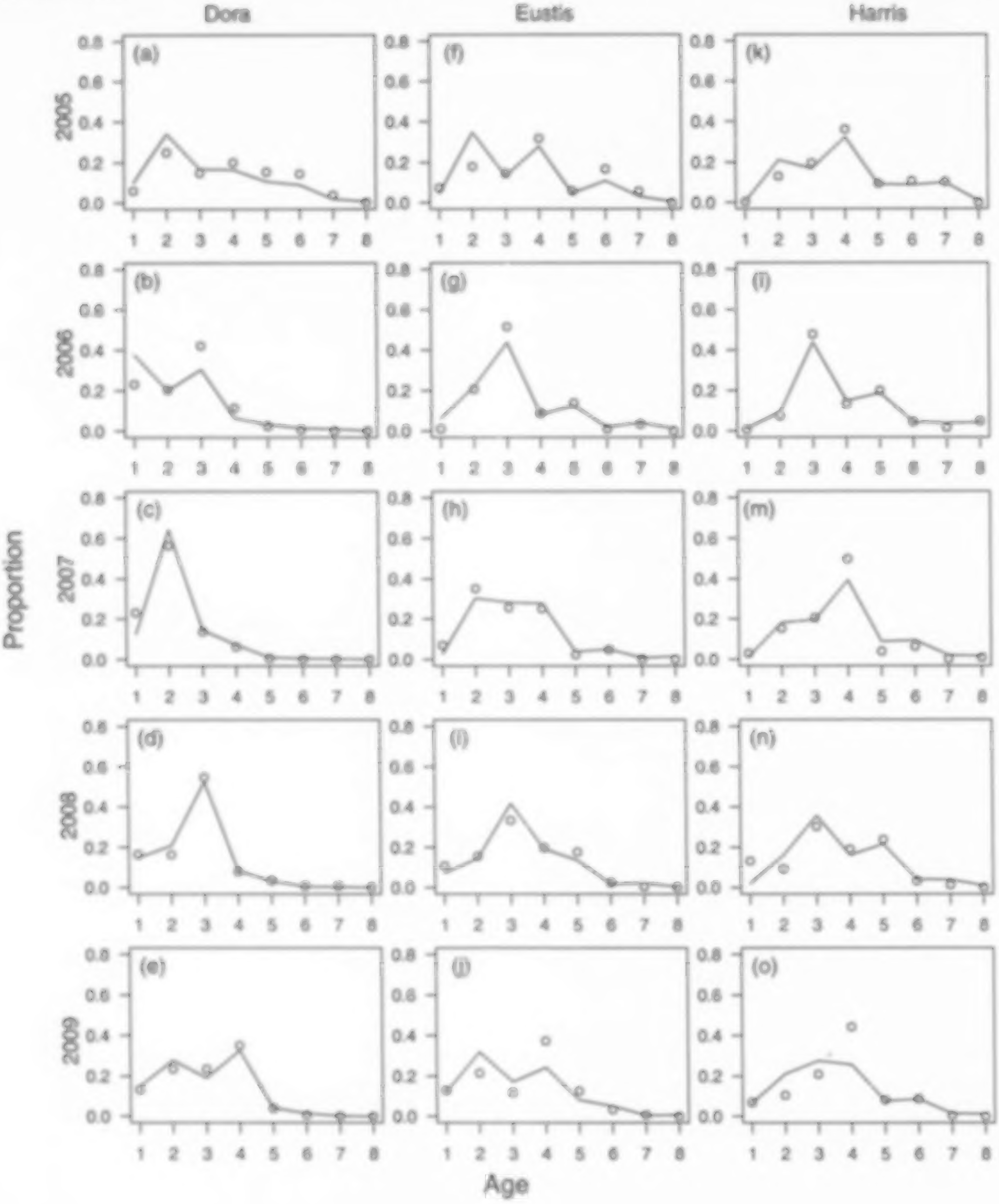
Recruitment

The length–age model fit the observed data reasonably well. Predicted catches at age in January (Fig. 1) and November (not shown) UF gill net surveys generally matched observed age proportions. Model-predicted length composition of the SJRWMD gill net surveys (Fig. 2) and the commercial harvest in 2005 and 2006 (not shown) fit the observed data. The estimated recruitment time series showed some degree of temporal synchrony in year class strength among lakes (Fig. 3). Lake Dora had strong age-1 recruitment in 2000 and 2006 (1999 and 2005 year classes; Fig. 3*a*). Lake Eustis had above average recruitment in 2000 as well, but also had high recruitment in 1999 and 2009 (Fig. 3*b*). Lake Harris had relatively large recruitments in 1999 and 2009 (Fig. 3*c*). The 2006–2008 post-manipulation year classes at Lake Dora showed no decline following density reduction but rather were near the long-term average recruitment for the time series, suggesting that the density reduction did not substantially affect recruitment (Fig. 3*a*). All other model parameter estimates are listed in Table 1.

Growth

Annual growth increments differed among ages, but not among lakes or with population biomass (Table 2). The model with age only had the best AIC support (Table 2; $\beta_0 = 5.64 \pm 0.08$; $\beta_{age} = -0.51 \pm 0.02$; df = 55; $R^2 = 0.89$). Fitting additional parameters for population biomass and lake was not justified based on AIC (Table 2). The best model (age) fit the data considerably better than the single parameter (null) model (Table 2). When biomass was included in the model, its association with growth increments was weak. For instance, regression coefficient of biomass was 0.09 ± 0.29 mm per unit biomass in the model containing age and density as main effects (ΔAIC = 1.9). Given that biomass was measured relative to the average biomass across years,

Fig. 1. Observed (dots) and predicted (lines) gizzard shad age composition (proportion) in annual gill net surveys carried out by the University of Florida in January/February. The columns of panel plots represent the different lakes: Lake Dora (*a–e*), Eustis (*f–j*), and Harris (*k–o*). The rows of plots are different years from 2005 (top row) to 2009 (bottom row). Predicted age composition was from a length and age based stock assessment model.

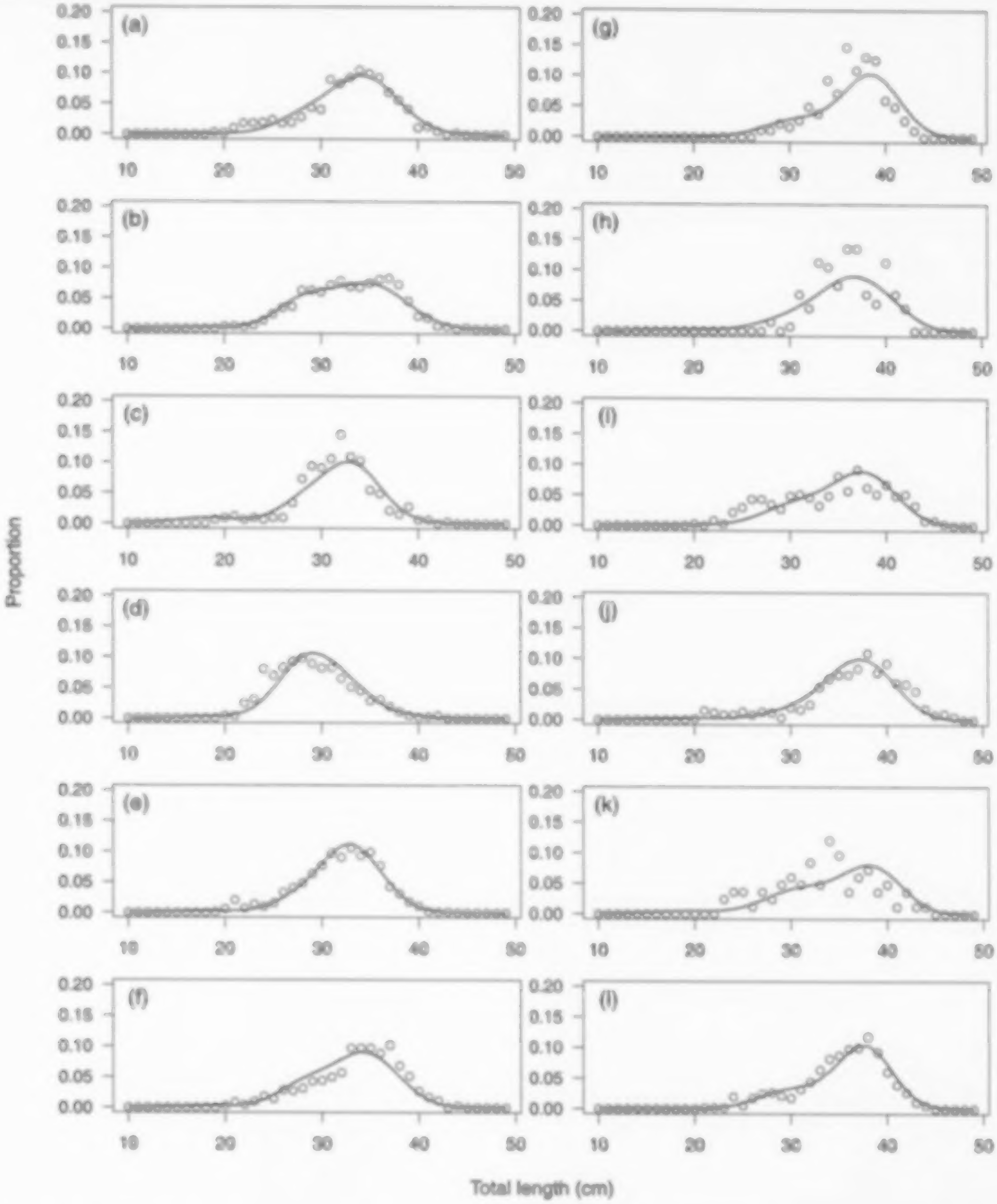


this coefficient suggests an 8-mm increase in annual growth increments with a 100% change in population density. Thus we conclude that growth was not density dependent and remained relatively constant throughout the time period at each of the lakes.

Maturity

Maturity was strongly related to GSI and there were no significant lake or lake × length effects. The best model had two parameters (intercept = −9.2 ± 2.53, slope (GSI) = 4.6 ± 1.28) on 94 residual degrees of freedom. The GSI (%)

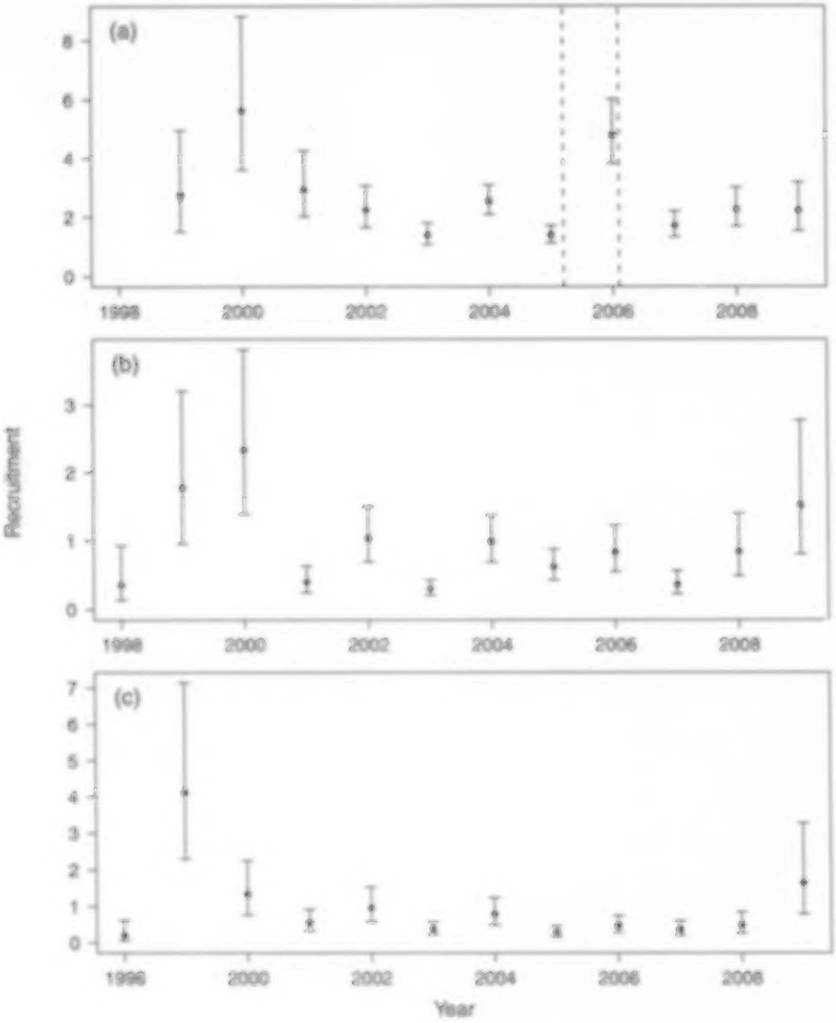
Fig. 2. Observed (dots) and predicted (lines) gizzard shad length composition (proportion) in annual gill net surveys carried out by the St. Johns River Water Management District in January/February. Lake Dora was sampled in 2003 (*a*), and 2005–2009 (*b*–*f*). Lake Eustis was sampled in 2003 (*g*) and 2006–2009 (*h*–*k*), and Lake Harris was sampled in 2003 (*l*). Predicted age composition was from a length and age based stock assessment model.



at which the model-predicted probability of maturity was 0.5, was 1.99%. Correct classification rates of mature and immature females were high. Ninety-three percent (45/48) of females classified by the model as mature were, in fact, mature, as indicated by histology. Likewise, 93% (45/48) of females classified as immature were, in fact, immature. Hence, female gizzard shad are likely to be mature if their GSI exceeds 2%. Because of the high classification rates, we were confident in extrapolating the model to other lakes and years to estimate maturity of females for which ovarian histology was not analyzed.

Fish length was a strong predictor of the probability of maturity. The minimum AIC model was an additive model with

Fig. 3. Annual age-1 recruitment estimates (±95% confidence interval, CI) from a length and age based stock assessment model for Lakes Dora (*a*), Eustis (*b*) and Harris (*c*). The units of the ordinate on (*a*) are millions of fish and the units on (*b*) and (*c*) are the number of recruits relative to the lake average. The vertical broken lines in the Lake Dora panel show the approximate timing of gizzard shad removals at Lake Dora.



length, lake, and cohort year as main effects ($\beta_0 = -10.89 \pm 0.78$; $\beta_{\text{length}} = 0.041 \pm 0.003$; $\beta_{\text{Eustis}} = -1.49 \pm 0.26$; $\beta_{\text{Harris}} = -1.57 \pm 0.31$; $\beta_{2004} = 0.09 \pm 0.31$; $\beta_{2005} = -0.95 \pm 0.25$; $\beta_{2006} = -0.15 \pm 0.40$; df = 1161; Table 2). This model was selected as the most parsimonious, and was used in subsequent calculations of spawner biomass (see below). Gizzard shad matured at a smaller size at Lake Dora (length at 50% maturity = 265 mm) than at Lakes Eustis (301 mm) and Harris (303 mm). Including cohort size and the biomass of age-2+ fish resulted in no improvement in AIC over the minimum AIC model. There was no significant relationship between length at 50% maturity and cohort size ($F = 0.87$, df = 10, $R^2 = 0.08$, $P = 0.37$; Fig. 4*a*) or gizzard shad biomass ($F = 0.95$, df = 10, $R^2 = 0.09$, $P = 0.35$; Fig. 4*b*).

Prerecruit survival

Spawner biomass at Lake Dora decreased to 28% of the average unharvested biomass in 2006 following the second year of harvest (Fig. 5). This reduction exceeded the natural variation in spawner biomass observed at unharvested lakes (Fig. 5). Spawner biomass decreased steadily from 2003–2008 at unharvested Lake Harris, owing to natural mortality of a large year class in 1999. Prerecruit survival was greatest at Lake Dora in 2005–2007, just after density reduction as recruitment was near the long-term average despite substantially reduced spawner biomass. However, prerecruit survival at Lake Dora after density reduction was exceeded by survival rates at Lake Harris in 2008 (Fig. 6).

Table 1. Parameter estimates (95% CI) from the length–age model for lakes Dora, Eustis, and Harris.

Parameter	Description	Dora	Eustis	Harris
M	Instantaneous natural mortality	0.94 (0.86–1.02)	1.02 (0.92–1.13)	1.07 (0.99–1.16)
K	von Bertalanffy growth coefficient	0.61 (0.60–0.63)	0.70 (0.66–0.74)	0.76 (0.73–0.79)
L_∞	Asymptotic length	387.89 (385.08–390.73)	406.85 (401.87–411.89)	389.67 (386.91–392.45)
t_0	Time at zero length	0.16 (0.13–0.18)	0.34 (0.29–0.40)	0.39 (0.34–0.44)
λ_1	CV in length at age coefficient	30.86 (30.43–31.29)	33.80 (32.86–34.77)	30.39 (29.17–31.66)
λ_2	CV in length at age coefficient	0.06 (0.04–0.09)	–0.19 (–0.24 to –0.14)	–0.11 (–0.16 to –0.05)
$L50_{UF}$	Length at 50% gear selectivity*	462.45 (445.64–479.89)	440.15 (428.78–451.82)	471.28 (460.62–482.19)
γ_{UF}	Gear selectivity coefficient*	0.84 (0.71–0.97)	0.65 (0.56–0.74)	0.81 (0.62–1.00)
β_{UF}	Gear selectivity coefficient*	0.09 (0.04–0.2)	0.06 (0.05–0.08)	0.14 (0.05–0.40)
$L50_{SJ}$	Length at 50% gear selectivity†	319.46 (312.66–326.42)	395.05 (374.20–417.07)	
γ_{SJ}	Gear selectivity coefficien†	0.00 (0.00–0.00)	0.00 (0.00–0.00)	
β_{SJ}	Gear selectivity coefficient†	0.04 (0.03–0.04)	0.03 (0.03–0.03)	
σ_R	Error standard deviation in recruitment		0.61 (0.40–0.92)	0.77 (0.50–1.18)
$L50_{05}$	Length at 50% gear selectivity‡	357.80 (340.36–376.13)		
β_{05}	Gear selectivity coefficient‡	0.04 (0.03–0.06)		
γ_{05}	Gear selectivity coefficient‡	0.00 (0.00–0.00)		
$L50_{06}$	Length at 50% gear selectivity§	300.86 (297.06–304.70)		
β_{06}	Gear selectivity coefficient§	0.15 (0.11–0.21)		
γ_{06}	Gear selectivity coefficient§	0.00 (0.00–0.00)		

*University of Florida gill-net survey.

†St. Johns River Water Management District gill-net survey.

‡2005 fishery.

§2006 fishery.

Prerecruit survival was negatively related to spawner biomass across lakes and years (Fig. 6). The most parsimonious model when fitting to the point estimates of prerecruit survival and spawner biomass included additive effects of spawner biomass and year (Table 2; $\beta_0 = -2.73 \pm 0.86$; $\beta_S = -1.68 \pm 0.58$; $\beta_{2004} = -0.99 \pm 0.39$; $\beta_{2005} = -0.44 \pm 0.44$; $\beta_{2006} = -1.12 \pm 0.53$; $\beta_{2007} = -0.77 \pm 0.55$; $\beta_{2008} = -0.16 \pm 0.52$; df = 11; $R^2 = 0.58$) . The point estimate of α (maximum prerecruit survival as spawner biomass approaches zero; i.e., exp(β0) was 0.07 from the best fitting model.

Lake-specific estimates (median of the posterior samples from the MCMC) of the maximum lifetime reproductive rate, $\widehat{\alpha}$, were 6.5 at Lake Dora, 6.3 at Lake Eustis, and 4.8 at Lake Harris. Variability in $\widehat{\alpha}$ among lakes was due to variation in equilibrium lifetime spawners per recruit, ϕ_0 among lakes (Lake Dora, 153.8; Lake Eustis, 140.7; Lake Harris, 106.4). This variation resulted primarily from differences in length at maturity, with Lake Dora having the smallest length at 50% maturity and therefore the largest ϕ_0, which resulted in a larger $\widehat{\alpha}$ estimate. An $\widehat{\alpha}$ estimate of 1.0 results in a linear relationship between prerecruit survival and spawner biomass, and signifies a lack of density dependence in prerecruit survival. Examination of 95% confidence intervals indicated that a value of 1.0 was not contained in the interval for any lake, indicating that a lack of density dependence in prerecruit survival was unlikely for these populations (Lake Dora 95% CI, 1.9–16.5; Lake Eustis 95%CI, 1.8–16.0; Lake Harris 95%CI, 1.4–13.3).

Monte Carlo simulations used to assess potential biases in α suggested that in the case of gizzard shad from these three lakes, time series bias and observation error in stock biomass would cause an underestimation of α rather than overestimation. These estimates of the maximum lifetime reproductive rate should therefore be viewed as conservative, which is preferable to an overly-optimistic estimate, from a management perspective.

Discussion

There are many studies showing increased prerecruit survival, increased growth and reduced size/age at maturity at low population densities in fishes, but there is debate about the relative importance of these mechanisms in fish compensation. Density-dependent changes in juvenile survival have been considered the primary mechanism for compensation in fish populations (Rose et al. 2001). For example, individual-based-model simulations by Cowan et al. (2000) indicated that density dependent feedbacks on recruitment are most likely during the late larval to early juvenile phase because of peak total cohort consumption rates during that phase. Conversely, Lorenzen and Enberg (2002) suggested that density dependence in adult growth alone could explain observed compensation in 9 of 16 exploited fish populations. They further postulated that density dependence in growth may be most important under moderate reduction in density but that increased prerecruit survival would be the dominant compensatory mechanisms at very low population sizes. Under moderate variation in population and spawner biomass across lakes/years in our study, growth and maturation schedules remained relatively unchanged. This suggests that changes in prerecruit survival may be important under moderate as well as severe reductions in population density. Identifying consistent patterns in the relative importance of density-dependent mechanisms across species/habitats may be elusive. Recent studies of multiple dependent compensatory mechanisms suggest that the relative contributions of these potential

Table 2. Akaike information criterion (AIC) and ΔAIC values for competing models describing associations between gizzard shad (1) growth increments and age, lake, and population density (i.e., total population biomass), (2) maturity and lake, population density (B_t), cohort size, year, and cohort, (3) prerecruit survival and spawner biomass (SB) and year.

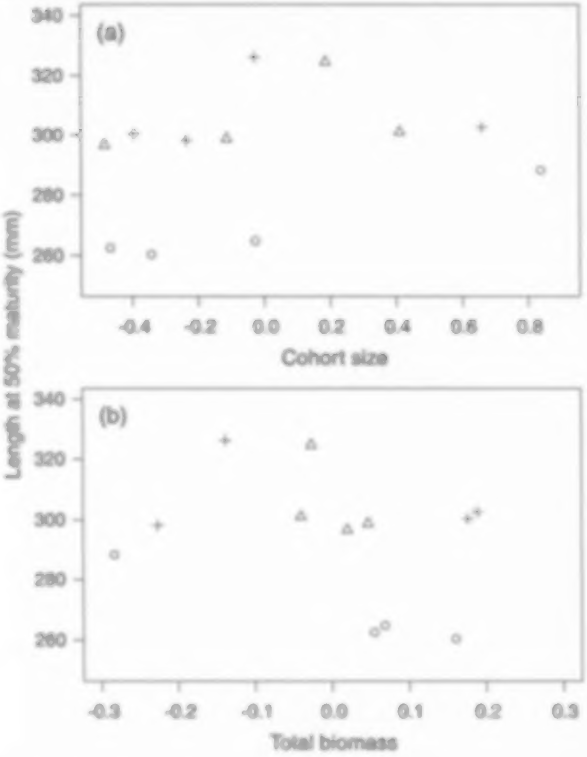
Model	AIC	ΔAIC
(1) Growth		
Age	5.5	0.0
Age+lake	7.2	1.7
Age+density	7.4	1.9
Intercept only (null)	130.7	125.2
(2) Maturity		
Length+lake+cohort year	605.4	0.0
Length+lake+cohort year+cohort size	605.4	0.0
Length+lake+cohort year+density	605.6	0.2
Length+lake+density	616.6	11.2
Length+lake+density+length×lake	619.1	13.7
Length+lake+density+cohort size	618.5	13.1
Length+lake	619.9	14.5
Length+lake+cohort size+length×lake	622.1	16.7
Length+lake+cohort size	620.2	14.8
Length+lake+lake×length	622.4	17.0
Length+density	665.0	59.6
Length	666.2	60.8
Length+cohort size	666.7	61.3
Intercept only (null)	1564.7	959.3
(3) Prerecruit survival		
SB+year	26.0	0.0
SB	31.9	5.9
Intercept only (null)	37.6	11.6

mechanisms may be species or population-specific (Vandenbos et al. 2006; Lorenzen 2008).

Recent meta-analyses have advanced our understanding of compensation in fish populations. Myers et al. (1999) and Goodwin et al. (2006) estimated the maximum lifetime reproductive rate, $\widehat{\alpha}$, for 237 and 54 stocks of commercially exploited fishes, respectively. We calculated an average $\widehat{\alpha}$ of 47 (95%CI, 10–84) across all stocks included in both studies. Clupeids had below-average maximum reproductive rates at 19.3 (95%CI, 13.4–25) across stocks, and no gizzard shad stocks were included in their analyses. The mean estimate for clupeids was greater than the upper 95% confidence interval for the maximum lifetime reproductive rate for gizzard shad from our study. Gizzard shad may have relatively weak compensation when compared to other clupeids. For example, most estimates of $\widehat{\alpha}$ come from stock recruitment data generated from stock assessment models applied to commercially exploited fish species. Such data could contain substantial uncertainty and possible biases from serial autocorrelation, error in spawner biomass estimates, and lack of contrast in the data (Walters and Martell 2004). We used a whole-lake density reduction along with unharvested populations to estimate $\widehat{\alpha}$, and quantified the uncertainty in this parameter, which may provide less biased estimates than those obtained from traditional stock assessments.

Goodwin et al. (2006) identified associations between life history characteristics and the strength of compensation. They found that fishes fall along a continuum of long-lived

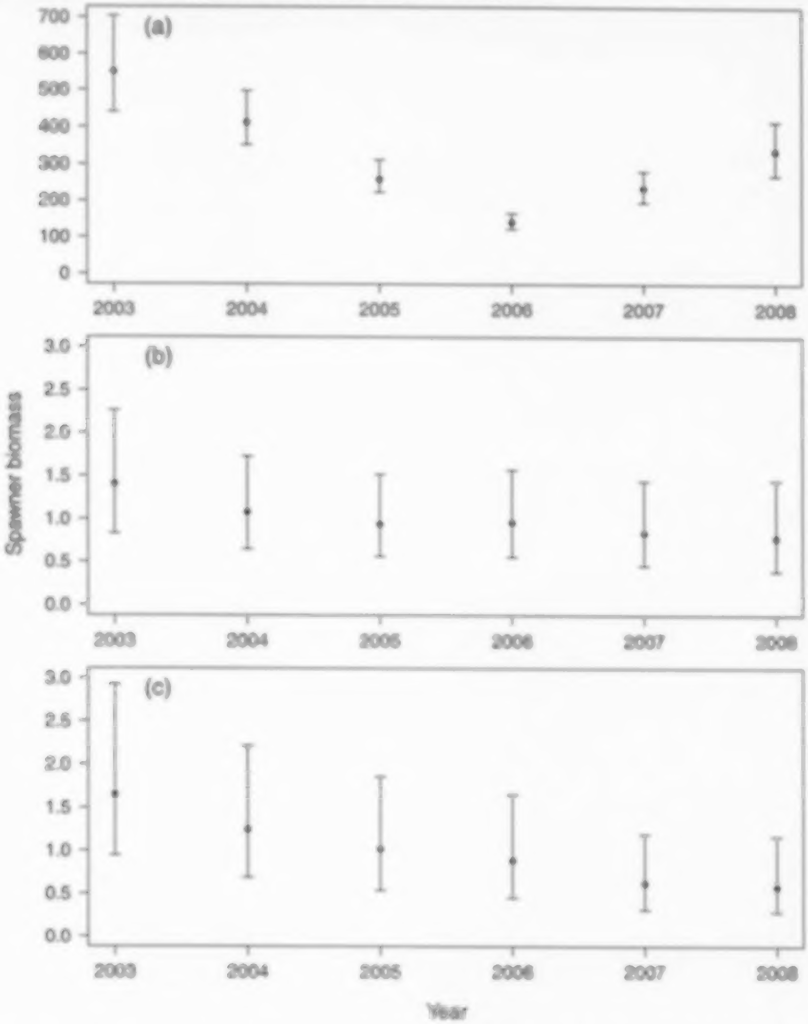
Fig. 4. Estimated length at 50% maturity for the 2003–2006 gizzard shad cohorts at lakes Dora (circle), Eustis (triangle), and Harris (square) plotted against (*a*) cohort size, and (*b*) the total biomass of age-2+ gizzard shad. Biomass and cohort size were estimated from a length and age based stock assessment model. Units of cohort size are the number of age-1 recruits rescaled to the lake-specific average. Units of biomass are metric tons rescaled to the lake-specific average.



highly-fecund species with low annual recruitment and strong compensation to short-lived, early-maturing species with high annual recruitment and weak density dependence. The former group exhibits a bet-hedging strategy to reproduce over many years, whereas the latter is adapted to quickly invade and exploit highly variable resources (Stearns 1992). Our data suggested that gizzard shad fall toward the short-lived, early maturing end of the spectrum, with fast growth, early maturation, and relatively weak density dependence in recruitment compensation.

Our study assessed the relative importance of density dependence of several demographic rates, but was unable to assess specific mechanisms influencing changes in those rates. We observed increased prerecruit survival at low spawner biomass, but this change could have been due to several mechanisms. Walters and Juanes (1993) proposed that reduced survival at high juvenile densities results from increased risk taking at small spatial and temporal scales by individuals attempting to procure scarce resources in a competitive environment. For example, juveniles may be forced to leave food-poor refugia and spend more time in predator-dense feeding zones to maintain adequate growth rates when cohort

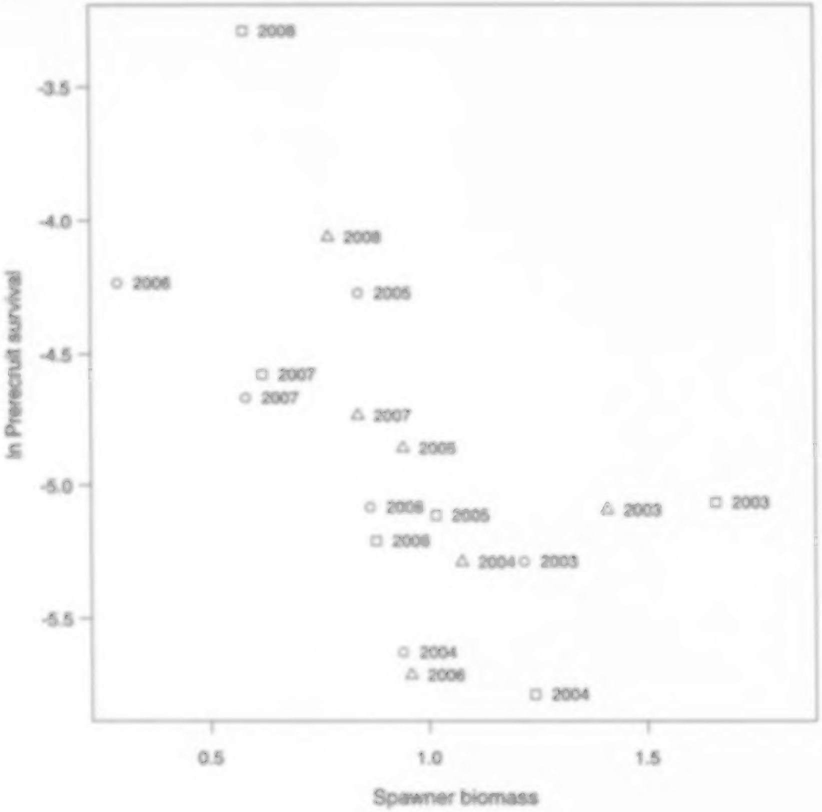
Fig. 5. Annual gizzard shad spawner biomass estimates (95% confidence intervals) at (*a*) Lakes Dora, (*b*) Eustis, and (*c*) Harris. Estimates were obtained from a length and age based stock assessment model. Units of spawner biomass for Lake Dora are metric tons whereas units for lakes Eustis and Harris are fish biomass relative to the average for the time series.



density is high. Density dependent growth rates of prerecruits may also affect survival rates. Numerous studies have shown increased predation risk for slower growing individuals within a cohort (reviewed by Sogard 1997). The "bigger is better" hypothesis (Shepherd and Cushing 1980) proposes that larger age-0 individuals have lower rates of mortality, because faster growth decreases the duration of exposure to stages where mortality is high (Houde 1987; Miller et al. 1988; Sogard 1997). Additional growth and survival studies on prerecruits are needed within the context of whole-lake density manipulations, to evaluate mechanisms for density-dependent survival that could not be addressed by our study.

We expected adult demographic rates, such as maturity and growth, to respond following density reduction. Substantial research has shown changes in these rates with changing density. Age at maturity, for example, generally decreases with increased exploitation (Trippel 1995). Rijnsdorp (1993) considered the exploitation of the North Sea plaice, *Pleuronectes platessa*, an experimental density manipulation, and reported decreases in length and age at maturity since 1900, and Beacham (1983) documented decreased age and size at maturity following exploitation. Shifts in maturation schedules may be controlled by feeding conditions during nutritionally limited periods in gametogenesis (Burton 1994). Populations with size-dependent maturation schedules may also undergo changes in age at maturity via increases in growth rate (Trippel 1995). Somatic growth typically increases when population density decreases, owing to decreased intraspecific competition. Many studies have documented increases in growth related to exploitation of fish stocks (Millner and Whiting 1996; Rijnsdorp and van Leeuwen 1996; Helser and Almeida 1997). Kim and DeVries (2000) reported substantial increases in age-0 gizzard shad growth following density reduction at Walker County Lake, Alabama, and Schaus et al.

Fig. 6. Natural log (ln) of prerecruit survival as a function of spawner biomass at lakes Dora (circles), Eustis (triangles), and Harris (squares). Survival and spawner biomass observations are point estimates from a length and age based stock assessment model. Spawner biomass has been rescaled to a mean unfished value of 1.0. Prerecruit survival is in units of the number of age-1 gizzard shad per unit spawner biomass. Cohort years are indicated.



(2002) found increased growth of gizzard shad at Acton Lake, Ohio, in years with low-population density. Thus, gizzard shad have clearly exhibited plasticity in growth in other systems. At Lake Dora, a highly productive system, perhaps intraspecific-competition during maturation was low even at the highest gizzard shad densities, thereby eliminating the possibility of density-dependent maturation responses.

The strength of manipulation should always be a consideration, and researchers should strive for large perturbations to elicit system responses (Carpenter 1989). In our study, size selective removal of gizzard shad reduced spawner biomass by approximately 70%. This corresponds to a spawning potential ratio (SPR) of 0.3, which would put many species at risk for recruitment overfishing (Mace 1994; Clark 2002). However, changes in total population biomass were only moderate (Catalano et al. 2010), owing to high estimated natural mortality, which caused a large proportion of the population to reside in young age classes that were invulnerable to harvest. Contrast in total population biomass was therefore less than the contrast in spawner biomass, which may have dampened growth and maturation responses. The change in total population biomass may not have been enough to elicit strong responses in growth and maturation. Nevertheless, the manipulation resulted in a substantial reduction in spawner biomass, which allowed estimation of density-dependent changes in prerecruit survival. Future density-reduction studies should achieve stronger total biomass reductions so that changes in all demographic rates can be evaluated.

There are few examples of whole-lake density manipulations to test fish compensatory responses. Healey (1978, 1980) manipulated densities of both lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) in a Canadian shield lake, and reported compensatory changes in growth, recruitment, and fecundity, but the magnitude of these changes was not proportional to the amount of density reduction. Experimentally manipulated populations of brook trout (*Salvelinus fontinalis*) have provided good insights into compensation. DeGisi (1994) manipulated seven lakes in the Sierra Nevada Mountains, California, and found that the maximum lifetime reproductive rate in these populations was approximately 19 (Myers 2002). Johnston and Post (2009) found density-dependent decreases in growth and survival, as well as increases in age at maturity of bull trout *Salvelinus confluentus* following a 28-fold increase in population density, owing to harvest restrictions at Lower Kananaskis Lake, Alberta, Canada. Tonn et al. (1994) reported a strong negative association between age-0 growth and survival and adult abundance for crucian carp (*Carassius carassius*) in experimentally stocked ponds. Manipulation of the Lake Dora gizzard shad population contributes substantially to the body of research on compensation. This study is unique because changes in demographic rates in the adult as well as prerecruit phase were assessed to evaluate the relative importance of the two life stages in density dependence. Our study provides empirical support that compensation in the larval/juvenile survival rates is an important population response to the harvesting of fish populations.

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Relative importance of size-based competitive ability and degree of niche overlap in inter-cohort competition of Atlantic salmon (*Salmo salar*) juveniles

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Abstract: The competitive effect of older cohorts on younger cohorts may strengthen with increasing size differences owing to increasing differences in competitive abilities. Alternatively, it may weaken owing to increasing partitioning of resources as a result of ontogenetic niche shifts. Here, we test this by creating spatial variation in densities of one size class of overyearling Atlantic salmon (*Salmo salar*) and assess the effects on two size classes of young-of-the-year (YOY). The positive relationship between growth of overyearlings and final body size of YOY (a proxy for their growth) was steeper for the larger size class of YOY than for the smaller size class, which would be expected if the degree of niche overlap between two cohorts depended on their size difference. The negative relationship between overyearling density and YOY body size was also steeper for the larger size class (at least for body mass), suggesting that effects of body size differences on relative competitive abilities appear to be of less importance than the effects on degree of niche overlap. YOY should thus experience relatively less competition from older cohorts in rapidly growing populations, and this may also apply to many other fish species with ontogenetic niche shifts.

Résumé : L'effet de compétition des cohortes plus âgées sur les plus jeunes peut s'accroître en fonction des différences de taille à cause des divergences croissantes entre leurs capacités compétitives. D'autre part, il peut diminuer à cause du partitionnement accru des ressources dû aux changements de niche au cours de l'ontogenèse. Nous testons ces assertions en créant une variation spatiale des densités d'une classe d'âge de saumons atlantiques (*Salmo salar*) âgés de plus d'un an et en évaluant les effets sur deux classes de taille de jeunes de l'année (YOY). La relation positive entre la croissance des poissons de plus d'un an et la taille finale des YOY (une variable de remplacement pour leur croissance) a une pente plus forte pour la classe de taille plus grande de YOY que pour la plus petite, ce à quoi on peut s'attendre si le degré de chevauchement des niches entre les deux cohortes dépend de leur différence de taille. La relation négative entre la densité des poissons de plus d'un an et la taille corporelle des YOY possède aussi une pente plus forte pour la classe de taille plus grande (au moins pour la masse corporelle), ce qui laisse croire que les effets des différences de taille corporelle sur les capacités relatives de compétition semblent être de moindre importance que les effets sur le degré de chevauchement des niches. Les YOY devraient ainsi subir relativement moins de compétition de la part des cohortes plus âgées dans des populations à croissance rapide; ce phénomène pourrait aussi s'appliquer à d'autres espèces de poissons qui font des changements ontogéniques de niche.

[Traduit par la Rédaction]

Introduction

For organisms that rely on resources that can be defended, body size is commonly a strong predictor of competitive dominance. For age-structured populations, this may cause the older cohort (because older individuals are larger) to have an advantage over the younger cohort (Schwinning and Weiner 1998; Schmitt and Holbrook 1999). If relative competitive abilities of individuals from two cohorts depend on their relative size difference, the effect of an older cohort on a younger cohort can be expected to increase with an increasing size difference. However, owing to ontogenetic niche shifts, size differences between cohorts may also translate into the partitioning of resources among them. Larger size differences between cohorts may then be expected to reduce niche overlap and, hence, cause reduced intensity of inter-cohort competition. This mirrors ideas found within the theoretical framework of community structure dealing with the role of species differences in influencing competitive effects.

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According to this, two species may coexist if they have a low degree of niche overlap or, alternatively, if they have only subtle niche differences but are similar in their competitive ability (Mayfield and Levine 2010). Because the two effects of size differences counteract each other, increasing the size difference between two cohorts may either increase or decrease the competitive effect of one on the other, depending on their relative importance.

Although the issue of inter-cohort competition is of relevance across a wide range of aquatic taxa (e.g., echinoderms (Nishizaki and Ackerman 2004), crustaceans (Aljetlawi and Leonardsson 2002), and amphibians (Eitam et al. 2005)), it has received particular interest in fish populations (e.g., Bjørnstad et al. 2004; Byström and Andersson 2005; Samhouri et al. 2009). Being ectothermic and showing indeterminate growth, fish populations and species may differ widely in the body size differences found among cohorts. Particularly, populations living close to their lower or upper thermal limits for growth may be expected to show relatively little difference in body size between consecutive cohorts. Depending on the importance of body size effects on competitive ability vs. niche use, a larger size difference between two cohorts may increase or decrease the strength of competition experienced by the younger cohort from the older cohort. However, none of the existing studies of inter-cohort competition have addressed the effect of the magnitude of size differences between cohorts.

Stream-living salmonid fishes represent a particularly tractable study system for manipulative field studies regarding inter-cohort competition. For many of these species, their population dynamics are highly influenced by intraspecific competition (reviewed by Elliott 1994; Einum and Nislow 2011; Nislow et al. 2011), and juveniles originating from several potentially competing cohorts live in sympatry. This is true even for some anadromous species, such as Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), which may stay as juveniles in the stream for up to 8 years before migrating to the sea (Thorstad et al. 2011). Older cohorts may have a negative effect on younger cohorts (Nordwall et al. 2001; Kaspersson and Höjesjö 2009) and vice versa (Kaspersson et al. 2010; Kvingedal and Einum 2011). Yet, it is not known how the intensity of inter-cohort competition may depend on their size difference. Here, we present results from a field study of juvenile Atlantic salmon where we created spatial variation in the density of overyearlings in the presence of two size classes of young-of-the-year (YOY). We first tested whether spatial patterns in growth were consistent with the assumption that the degree of niche overlap (i.e., similarity in resource requirements) between two cohorts decreases with increasing size difference. Two cohorts that have a high degree of niche overlap are expected to have a higher spatial correlation (i.e., covariation over space) in growth performance than two cohorts with less overlap. For the older age class, individual pit tags allowed us to measure growth rates directly, whereas final body size was used as a proxy for growth for the YOY size classes. We then tested whether the effect of local density per se of an older cohort on the growth of a younger cohort depended on the size difference. If the magnitude of competition experienced by the younger cohort from an older cohort was primarily driven by body size effects on competitive abilities, we predicted that a larger size difference between two cohorts caused a stronger effect of density of the older cohort on growth of the younger cohort. In contrast, if the magnitude of competition experienced by younger cohorts from older cohorts was primarily driven by degree of niche overlap, we predicted the opposite pattern to emerge, whereby a larger size difference between two cohorts caused a weaker effect of density of the older cohort on the growth of the younger cohort.

Materials and methods

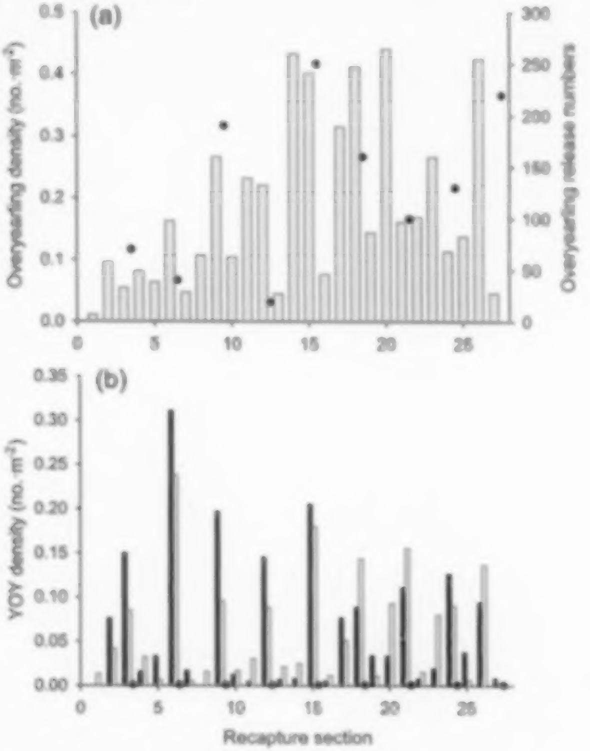
Study location and fish material

The study was conducted in the Stream Osalandsbekken, which is a small tributary (total length, ca. 3km and mean width, 3.8 m) to the River Imsa in southwestern Norway. The stream has a resident brown trout population but no naturally occurring Atlantic salmon owing to a barrier preventing upwards migration from the River Imsa. A total of 900 small YOY (mean ± SD, body length, 33 ± 2 mm and weight, 0.35 ± 0.05 g), 450 large YOY (62 ± 5 mm and 2.51 ± 0.52 g), and 1180 overyearling (i.e., 1+, 115 ± 13 mm and 16.66 ± 5.74 g) captively bred Imsa salmon were released. These were offspring from wild reared Imsa salmon parental fish that were caught in a fish trap at return to the River Imsa from the sea. Although hatchery-reared juveniles may initially use different habitats and diets compared with wild fish after they have been released, they rapidly adjust these to become more similar (reviewed in Einum and Fleming 2001) and, hence, constitute good model organisms to examine effects of body size differences on competitive effects. The difference in size between the small and the large YOY was due to incubation in ambient vs. heated water during incubation, and hence, they experienced different dates for the start of feeding. The two size classes were marked with single visible implant elastomers (Nortwest Marine Technology, Inc.) that were injected subcutaneously close to the dorsal fin using two different colours (red and yellow) for group identification at recapture. The YOY were divided into nine groups, each consisting of 100 small and 50 large YOY, and were released at nine sites situated ca. 150 m apart on 10 June 2005. The overyearlings were pit tagged and measured for length during 8–14 June 2005. Previous experiments in this system have shown that released salmonids tend to stay close to their release sites during their first summer (Einum et al. 2006; Skoglund et al. 2011), and this makes it possible to create spatial variation in their densities. Thus, overyearlings were divided into nine groups containing different numbers (20, 40, 69, 100, 130, 160, 190, 220, and 250 individuals), which were assigned to the same release sites as the YOY in a random fashion (Fig. 1). Half of the individuals in each of the overyearling groups were released in the stream together with the YOY on 10 June 2005, while the remaining fish were released 4 d later. The fish were transported in oxygenated water to the release sites and kept in enclosures in the stream for 3–4 h of habituation before being released.

Recaptures

Recapturing was performed by electrofishing in the period 5–8 September 2005. The stream was divided into 50 m sections, the first one starting 200 m below the lowest release

Fig. 1. Spatial distribution of Atlantic salmon releases (circles) and recaptures (bars) of (*a*) overyearlings and (*b*) young-of-the-year (YOY) along Stream Osalandsbekken. Recapture sections are numbered from the lowermost to upstream. Overyearling densities at recapture are shown together with overyearling release numbers at different locations. For YOY, all release sites received equal numbers and, hence, only their positions are indicated. For these, grey bars indicate the large YOY size class, and black bars indicate the small YOY size class.



site and the last one at an impassable waterfall 50 m above the uppermost release site. Depending on fish abundance and catchability, one to four electrofish passes were performed in each section. A total of 298 small YOY, 271 large YOY, and 540 overyearlings were recaptured. Brown trout captured during electrofishing were measured for length before being released back into the stream. Recaptured salmon were killed before transportation on ice to the lab for length and weight measurements.

Density estimates

Local population densities were estimated for YOY and overyearlings for each section by the Zippin procedure, based on successive removal of fish during electrofish passes (Bohlin et al. 1989). In sections where the total catch of a given cohort was 15 or less individuals (10 out of 27 sections), densities were estimated from average catchability. Separate densities for small and large YOY were calculated based on the total YOY density and the proportion of small and large individuals caught. Overyearlings were caught in all 27 sections, whereas small and large YOY were caught in 25 and 26 sections, respectively (Fig. 1). In our modelling, we assume that the estimated final densities reflect those experienced during the majority of the experimental period. A similar release study conducted in more controlled environments suggests that the majority of movements occur within the first 1–2 days following release, supporting our assumption (Robertsen et al. 2011).

Table 1. Effects of size class identity (S), young-of-the-year (YOY) salmon density (D_{YOY}), and overyearling salmon growth (G_o) on (*a*) final body length and (*b*) body mass of YOY Atlantic salmon across stations in Stream Osalandsbekken as estimated from linear mixed effects models with stations as a random effect.

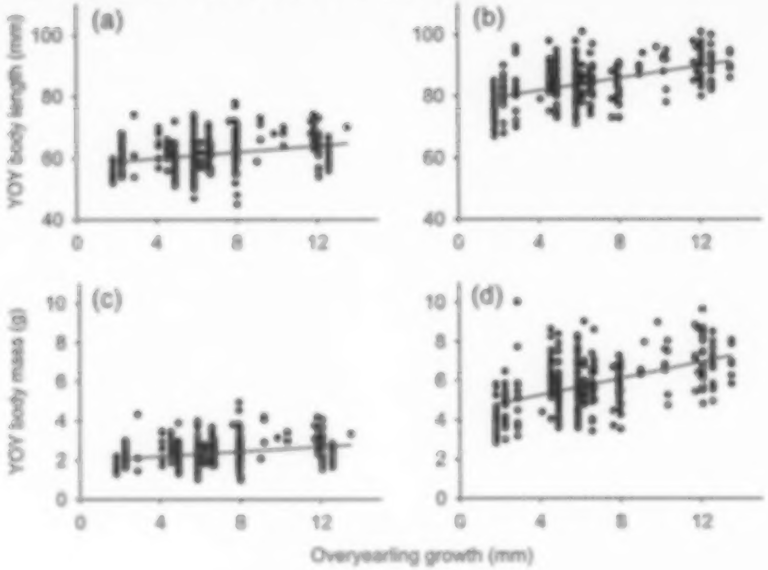
	$\beta \pm$ SE	df	t	P
(*a*) Length				
Intercept	61.11±1.65	525	36.96	<0.001
S^*	17.31±1.52	525	11.36	<0.001
D_{YOY}	−11.19±3.75	24	−2.98	0.007
G_o	0.49±0.16	24	3.06	0.005
$S^* \times D_{YOY}$	8.35±3.16	525	2.64	0.009
$S^* \times G_o$	0.53±0.15	525	3.54	<0.001
(*b*) Mass				
Intercept	2.36±0.24	526	9.89	<0.001
S^*	2.49±0.19	526	13.35	<0.001
D_{YOY}	−1.43±0.55	24	−2.59	0.016
G_o	0.06±0.02	24	2.64	0.015
$S^* \times G_o$	0.14±0.03	526	5.58	<0.001

*Parameters give values for large YOY relative to small YOY.

Statistical analyses

We first tested whether spatial patterns in growth were consistent with the degree of niche overlap between two cohorts being dependent on their size difference. In our model, we evaluated the effects of size group identity (small or large YOY), YOY density, and overyearling growth (i.e., final length – initial length) on YOY final size. The latter measure represents a proxy for YOY growth, since these were not individually marked. Overyearling growth, which incorporates effects of both intrinsic environmental factors (i.e., habitat variables) and fish density, is a good proxy for overyearling habitat quality. In our data, mean overyearling growth and overyearling density were negatively correlated among sections ($n = 27$, $r = -0.56$, $P = 0.002$), but much residual variation existed suggesting an important role for intrinsic environmental factors influencing growth. In addition to the main effects of these factors, we allowed for interactions between size group and YOY density and between size group and overyearling growth. The latter of these indicates whether the spatial relationship between growth of the older cohort, and hence their experienced habitat quality, and the younger cohort depended on the size class of the younger cohort. Separate effects of densities of small and large YOY on their own final size could not be estimated owing to their strong spatial correlation ($N = 27$, $r = 0.85$, $P < 0.001$) and corresponding high colinearity (VIF = 3.6, Zuur et al. 2010). A single estimate of YOY density including both size classes was, therefore, used in the model. Other sources of spatial variation in final YOY size (e.g., habitat quality and trout abundance) were accounted for by including section number

Fig. 2. Relationship between local overyearling growth (in mm) and young-of-the-year (YOY) body length (*a* and *b*) or body mass (*c* and *d*) in small (*a* and *c*) and large YOY (*b* and *d*) of Atlantic salmon across sampled sections in Stream Osalandsbekken. Regression lines are fitted for illustration only; for parameter estimates from mixed effects models see Table 1.



as a random factor (i.e., random intercept). Thus, the full model can be expressed as:

$$(1)\qquad \text{YOY size}_{ij} = \alpha + \beta_1 S_i + \beta_2 D_{\text{YOY}j} + \beta_3 G_{oj} + \beta_4 S_i \times D_{\text{YOY}j} + \beta_5 S_i \times G_{oj} + b_j + \varepsilon_{ij}$$

where S indicates which size group the YOY belongs to, D_{YOY} denotes the density of YOY, G_o indicates the mean growth of overyearling salmon, i is an individual index, j is a section index, and the term b_j represents the random section effect. For YOY size we modelled both final body length and wet body mass. We fitted these mixed effects models with the lme function within the nlme package (Pinheiro et al. 2009). The residuals from this model plotted against section suggested no spatial pattern and satisfied assumptions of normality and homogeneity for analysis of final body length. There was a significant negative correlation between YOY density and overyearling growth (N = 27, r = –0.41, P = 0.034), but this was not sufficiently strong to produce problems regarding colinearity (VIF = 1.2). For final wet mass, larger residuals were observed for large YOY than for small YOY. We, therefore, applied the varIdent function within the nlme package to allow for different variance between YOY size classes in this analysis. We proceeded using this random structure and compared different fixed effects structures by a backwards selection procedure and comparisons of log likelihoods of alternative models (calculated based on ML (Zuur et al. 2009)).

We then tested whether the effect of local density per se of an older cohort on the growth of a younger one depended on the size difference between the two. This was done by repeating the above modelling (eq. 1), but this time replacing overyearling salmon growth with overyearling salmon density (D_o) and, hence, allowing variation in YOY body size among sections owing to effects of intrinsic environmental quality to be incorporated in the model as a random effect. There was a tendency for YOY and overyearling densities to be spatially correlated (N = 27, r = 0.37, P = 0.057), but again, this did not introduce problems regarding colinearity (VIF = 1.2).

All statistical analyses were conducted using the statistical software R version 2.11.1 (R Development Core Team 2009).

Results

Estimated densities for the different recapture sections ranged from 0 to 0.31 m^{-2} for small YOY, from 0 to 0.24 m^{-2} for large YOY, and from 0.01 to 0.44 m^{-2} for overyearlings (Fig. 1). Mean body length ± SD at recapture was 61 ± 6 mm, 84 ± 7 mm, and 121 ± 11 mm for small YOY, large YOY, and overyearlings, respectively.

Effects of overyearling growth

For YOY body length, neither of the two interaction terms could be removed from the model (eq. 1) without causing a significant decrease in log likelihoods (P <0.009 for both). YOY body length decreased with YOY density and increased with overyearling growth (Table 1). In addition, the interaction terms showed that the effect of YOY density was higher for the smallest YOY, whereas the effect of overyearling growth was highest for the largest YOY (Table 1*a*; Figs. 2*a* and 2*b*).

For YOY body mass, the interaction term between YOY size class and YOY salmon density could be removed (P = 0.07). In contrast, the interaction between YOY size class and overyearling growth could not be removed (P < 0.001), nor could the main effect of YOY density (P = 0.009). The effect of overyearling growth was largest for the large YOY (Table 1*b*; Figs. 2*c* and 2*d*).

Effects of overyearling density

For YOY body length, both interaction terms could be removed from the model without causing a significant decrease in log likelihoods ($P > 0.10$ for both). However, when analysing the data for YOY size classes separately, the main effect of overyearling density could be removed from the model for small YOY ($P = 0.054$), but not for large YOY ($P < 0.001$; parameter estimate, $\beta = -16.02 \pm 4.68$). The main effects of YOY or overyearling density could not be removed ($P < 0.015$ for both). YOY body length decreased with increasing YOY and overyearling density (Table 2*a*; Figs. 3*a* and 3*b*).

For YOY body mass, the interaction term between YOY size class and YOY salmon density could be removed ($P = 0.64$). In contrast, the interaction between YOY size class and overyearling density could not be removed ($P = 0.025$), nor could the main effect of YOY density ($P = 0.004$). YOY wet mass decreased with YOY density (Table 2). The interaction term indicated a more negative effect of overyearling density on size of the largest YOY size class than on the smaller one (Table 2*b*; Figs. 3*c* and 3*d*). To evaluate whether the existence of inter-cohort competition may depend qualitatively on the chosen sizes of cohorts, we repeated the modelling regarding effects of local density of an older cohort on final body mass but separately for small and large YOY. For small YOY, the effect of overyearling density could be removed from the model ($P = 0.233$), whereas YOY density could not ($P < 0.001$) and negatively influenced final body mass ($\beta = -2.11 \pm 0.59$, $t = -3.57$, $P = 0.002$). In contrast, for large YOY, overyearling density could not be removed from the model ($P = 0.016$), whereas YOY density could ($P = 0.127$). Thus, overyearling density negatively influenced final body mass of large YOY ($\beta = -3.44 \pm 1.42$, $t = -2.42$, $P = 0.023$).

Table 2. Effects of size class identity (S), young-of-the-year (YOY) salmon density (D_{YOY}), and overyearling salmon density (D_o) on (*a*) final body length and (*b*) body mass of YOY Atlantic salmon across stations in Stream Osalandsbekken as estimated from linear mixed effects models with stations as a random effect.

	$\beta \pm$ SE	df	t	P
(*a*) Length				
Intercept	67.43±1.27	527	52.89	<0.001
S[a]	23.20±0.49	527	47.82	<0.001
D_{YOY}	−11.30±4.90	24	−2.41	0.024
D_o	−12.78±4.90	24	−2.61	0.015
(*b*) Mass				
Intercept	3.15±0.19	526	16.56	<0.001
S[a]	3.79±0.19	526	20.10	<0.001
D_{YOY}	−2.05±0.70	24	−2.91	0.008
D_o	−0.83±0.76	24	−1.10	0.282
S[a] × D_o	−1.51±0.68	526	−2.24	0.026

[a] Parameters give values for large YOY relative to small YOY.

Discussion

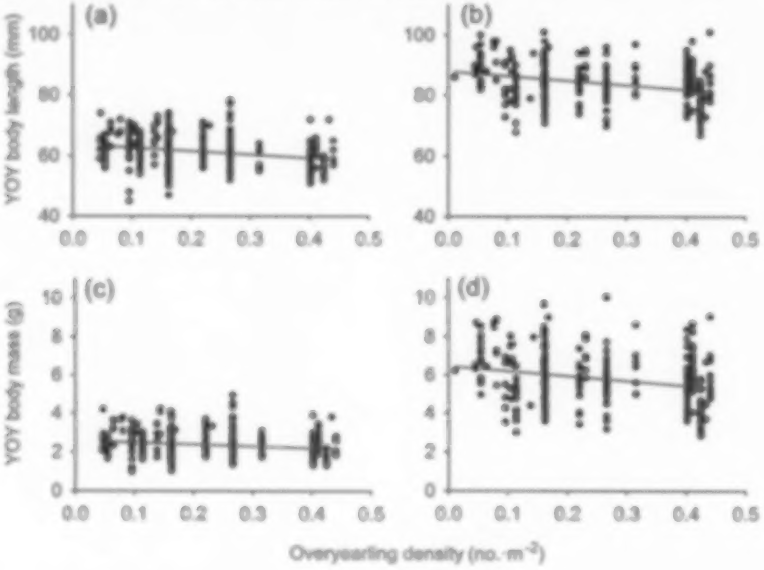
The results of the present study show how the difference in body size between juvenile cohorts of Atlantic salmon influences the effect of interactions between them. The positive relationship between growth of overyearlings and final body size (body length or mass, our proxies for YOY growth) of YOY was steeper for the larger size class of YOY than for the smaller size class. Thus, sections in the stream providing good growth conditions for overyearlings are also favourable for YOY, but more so for the larger YOY. This is consistent with the degree of niche overlap between two cohorts being dependent on their size difference, since two cohorts that have a high degree of niche overlap can be expected to have a higher spatial correlation in growth performance than two with less overlap.

At least two mechanisms may explain this observed pattern for juvenile Atlantic salmon. First, their requirements for physical habitat changes rapidly during the first summer. An empirically validated bioenergetics model suggests that suitable habitats differ among small and large juveniles during their first summer of growth (Nislow et al. 1999, 2000), with the earliest stage following emergence from nests (1–2 months, equivalent to body sizes up to 1 g) requiring a narrow range of particularly slow water currents. Hence, the small YOY used here (with mean initial body mass of 0.35 g) would be expected to differ substantially from the large YOY in water current requirements. Larger juveniles typically utilize faster flowing, deeper water and require coarser substrate (reviewed by Armstrong et al. 2003), and subsequent changes in habitat requirements from large YOY to overyearling sizes are likely less dramatic. Second, the degree of diet overlap can also be expected to decrease with increasing size difference, since the mean prey size ingested by the juveniles increase with their body size (Keeley and Grant 1997).

Given an effect of the size difference between two cohorts on the degree of niche overlap, a smaller size difference is expected to cause a stronger competitive effect of the older cohort on the younger one. Alternatively, competitive effects may be mostly influenced by the effect of size differences on competitive abilities, with a large size difference conferring a larger competitive advantage on the older cohort. Our results suggest that for Atlantic salmon, effects of body size differences on relative competitive abilities (Abbott et al. 1985; Cutts et al.1999) are of less importance than the effects on degree of niche overlap. This result was strong with respect to YOY body mass, which was negatively related to overyearling density for large but not small YOY. For YOY body length, the interaction term between size class and overyearling density could be removed from the model. However, the tendency was also in the same direction for this trait. Furthermore, a tendency in the opposite direction, with stronger effects of overyearlings on small than large YOY, would be expected if relative competitive abilities were more important. Thus, based on these findings, competitive effects of overyearling salmon on YOY growth appear to be mostly influenced by the degree of niche overlap and less by effects of size differences on competitive abilities.

The observed effects on growth are likely to be accompanied by survival effects. Although correlations between body size and survival in juvenile salmonids during winter can be variable and even negative (Hendry et al. 2003; Carlson et al. 2004, 2008), a reduced growth rate will inevitably lead to increased age and (or) reduced size at sea migration. Everything else being equal, an increased age at sea migration will cause an increased accumulated mortality during the fresh-

Fig. 3. Relationship between local overyearling density and young-of-the-year (YOY) body length (*a* and *b*) or body mass (*c* and *d*) in small (*a* and *c*) and large YOY (*b* and *d*) of Atlantic salmon across sampled sections in Stream Osalandsbekken. Regression lines are fitted for illustration only; for parameter estimates from mixed effects models see Table 2.



water stage, whereas a reduced size at sea migration is expected to increase mortality at sea (e.g., Jokikokko et al. 2006). Thus, reduced growth rates due to inter-cohort competition are predicted to cause increased mortality rates up to maturity.

Based on the present results, competitive effects of overyearlings on YOY are predicted to be strongest in slow growing populations where these differ little in body size. As for most fish species, the growth rates of stream-living salmonids vary substantially among populations, with the majority of this variation being attributed to variation in water temperatures (Jensen et al. 2000). As a result, the mean size of 1-year-old fish can differ by almost one order of magnitude (e.g., 1.4 g vs. 10.5 g for brown trout in the two Norwegian Rivers Kobbelva and Batnfjordselva, Jensen et al. 2000), and this will clearly have consequences for the intensity of competition they impose upon the YOY. This will be particularly true during the early YOY stages when their body size is mainly determined by egg size, which varies relatively little among populations (Fleming 1996). Differences in growth rate among populations may also explain why some studies have been able to detect intercohort competition between YOY and older salmonid cohorts (Nordwall et al. 2001; Kaspersson and Höjesjö 2009), whereas others have not (Elliott 1985), although such studies often also differ widely in their approach. According to our findings, YOY Atlantic salmon should experience relatively less competition from older cohorts in more southern, warmer rivers that provide rapid growth.

Inter-population differences in intensity of inter-cohort competition may also be expected to be present in other fishes, as well as in other types of age-structured organisms where ontogenetic niche shifts are present and where growth rates vary among populations. Interestingly, theoretical developments suggest that inter-cohort competition that favours older and larger individuals contributes to stabilizing population dynamics (Persson et al. 2000; Aikio and Pakkasmaa 2003). Thus, one prediction arising from the present study is that population stability should vary across gradients in growth rates owing to effects on intensity of inter-cohort competition. Furthermore, for organisms where growth trajectories vary widely among populations owing to environmental differences, human activities and climate change may indirectly influence the intensity of inter-cohort competition. If so, this adds complexity to the population dynamics of age-structured populations.

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Coupling genetic and otolith trace element analyses to identify river-born fish with hatchery pedigrees in stocked Atlantic salmon (*Salmo salar*) populations

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Abstract: This study combines otolith trace element and genetic analyses to explore the origin of individuals when hatchery-reared fish are released into wild populations. We sampled 90 juvenile Atlantic salmon (*Salmo salar*) in four rivers in Normandy (France) and in the hatchery stock. Individuals were analyzed at six microsatellite markers and their otolith elemental concentrations (14 elements) were measured using femto-second laser ablation inductively-coupled plasma mass spectrometry. Wild populations were genetically differentiated from the hatchery strain ($F_{ST} \approx 0.06$). Significant differences in elemental concentrations were found among otoliths of juveniles from the four rivers and the hatchery, allowing the identification of their geographic origin (83%–100% correct assignment). Coupling genetic and trace element analyses on the same individuals provided formal evidence that hatchery-born juveniles released into the wild can migrate to the sea and return as adults to breed on natural spawning grounds. Their progeny have pure hatchery pedigrees but have otoliths typical of river-born juveniles, meaning that they can be mistaken for hatchery-raised juveniles if only genetic data are considered. The presence of hybrids also confirmed that individuals with hatchery pedigrees can breed with wild conspecifics.

Résumé : Notre étude combine des analyses d'éléments en trace dans les otolithes et des analyses génétiques pour déterminer l'origine des individus lorsque des poissons élevés en pisciculture sont relâchés dans des populations sauvages. Nous avons prélevé 90 jeunes saumons atlantiques (*Salmo salar*) dans quatre rivières de Normandie (France) et dans le stock de pisciculture. Chez ces individus, nous avons analysé six marqueurs microsatellites et déterminé les concentrations en éléments (14 éléments) de leurs otolithes par spectrométrie de masse à plasma à couplage inductif avec ablation au laser femtoseconde. Généralement, les populations sauvages se différencient génétiquement de la souche de pisciculture ($F_{ST} \approx 0,06$). Il existe des différences significatives dans les concentrations d'éléments dans les otolithes des jeunes des quatre rivières et de la pisciculture, ce qui permet l'identification de leur origine géographique (83–100 % des assignations correctes). Le couplage des analyses génétiques et des dosages d'éléments en trace sur les mêmes individus fournit des preuves formelles que les jeunes nés en pisciculture et libérés en nature peuvent migrer en mer et revenir comme adultes se reproduire sur les sites naturels de fraie. Leurs rejetons possèdent des pedigrees purs de pisciculture mais des otolithes typiques de jeunes nés en rivière, ce qui veut dire qu'ils peuvent être confondus avec des jeunes élevés en pisciculture, si on ne considère que les données génétiques. La présence d'hybrides confirme de plus que des individus possédant un pedigree de pisciculture peuvent se reproduire avec des poissons sauvages de même espèce.

[Traduit par la Rédaction]

Introduction

The supplementation of wild populations with hatchery-reared individuals is a common practice in salmonid fisheries management (Aprahamian et al. 2003; Fraser 2008). The mortality of stocked fish is often supposed to be elevated, given the relatively low percentages of released individuals returning to target rivers (Ruzzante et al. 2004). It has also been shown that stocked fish are more likely to stray than wild conspecifics when coming back to freshwater spawning grounds (Jonsson et al. 2003; Pedersen et al. 2007). Wild and stocked fish can breed together, but detrimental effects of stocking on native stocks have been reported, notably a fitness decline of wild populations (Youngson and Verspoor 1998; Jonsson and Jonsson 2006; Araki et al. 2007).

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The use of natural marks detected by genetic and chemical analyses allows the quick assignment of fish to their natal population with a relatively high accuracy. Assignment methods based on multilocus genotypes and Bayesian algorithms (Pritchard et al. 2000; Corander et al. 2003) have a large potential for identifying the geographic origin of individuals (Manel et al. 2005; Hauser et al. 2006). For instance, Griffiths et al. (2010) gathered a large amount of genetic data from western Europe salmon populations, which can be used to identify individuals of unknown origin. Multilocus genotypes were also successfully used to identify hatchery-reared individuals and to study the hybridization between wild and hatchery fish in stocked rivers (Vasemägi et al. 2001; Aurelle et al. 2002; Hansen 2002). However, nonnative stocked individuals can breed together in natural environments and produce river-born juveniles with hatchery pedigrees (Hansen 2002; Araki et al. 2007; Hansen et al. 2009). Such individuals with hatchery pedigrees can, thus, either originate from the hatchery or from the breeding of hatchery-born adults that reproduced in the river.

In contrast with genetic characteristics, geochemical signatures from fish otoliths and scales are to a large extent not inherited from parents, but influenced by the local environment, especially elements in the water (Thorrold et al. 1997; Campana 1999). Therefore, variations in environmental chemistry represent natural tracers for fish origin and movements when the elemental composition of otoliths can be examined (Elsdon and Gillanders 2004; Friedrich and Halden 2008). Otolith trace-element and stable-isotope analyses have been successfully used to discriminate fish stocks, even at small spatial scales (Thorrold et al. 2001; Tomas et al. 2005; Veinott and Porter 2005), and to distinguish wild from hatchery-reared fish (Sohn et al. 2005; Gao and Bean 2008; Gibson-Reinemer et al. 2009). The alternative use of scales is tricky, since the inner portion of scales corresponding to juvenile growth includes collagen that is formed later in life (Hutchinson and Trueman 2006). As a result, the continuous growth and concentric aggregation of material in the otolith make it more appropriate to study the early life history of fish (but see Adey et al. 2009).

Several recent studies have demonstrated how joint genetic and otolith analyses can be useful for stock identification (Miller et al. 2005; Higgins et al. 2010; Smith and Campana 2010) and to explore patterns of dispersal in fish (Bradbury et al. 2008; Ohara et al. 2009). In the present work, we studied four Atlantic salmon (*Salmo salar*) populations from the Bay of Mont-Saint-Michel (France), which have been moderately to heavily stocked over the past decades. Joint otolith trace element (femto-second laser ablation inductively coupled mass spectrometry) and molecular (microsatellite markers) analyses were carried out on juveniles and adults collected in the wild and in the hatchery. Our objectives were to (*i*) investigate whether natal rivers of wild individuals can be identified, (*ii*) discriminate wild and hatchery-born individuals as well as their hybrids, and (*iii*) distinguish hatchery-born and river-born individuals among the fish with hatchery pedigrees.

Materials and methods

Study populations and restocking program

Four rivers located in the Bay of Mont Saint-Michel (Normandy, France) were studied: Sienne, Sée, Sélune, and Couesnon (Fig. 1). These rivers have been stocked for years with 10-month-old juveniles produced at the Favot Hatchery, Brittany, France (Fig. 1). These juveniles were the progeny of spawners caught every year in the Aulne River (Fig. 1) and were released after artificial breeding. Consequently, there were no otoliths of adults from the hatchery available for elemental analysis in our study. Earlier investigations on the genetic structure of French Atlantic salmon populations, using 17 microsatellites, revealed a significant differentiation between rivers from Brittany and Normandy (Perrier et al. unpublished data, 2010). Therefore, we expected individuals originating from Brittany to be readily identified among fish collected in Normandy rivers, based on microsatellite data analyses. Hatchery data indicate that a total of 333 700 juveniles were released into the Sélune River from 1989 to 1997. In the Couesnon River, 674 724 individuals were stocked from 1989 to 2007. The Sée and Sienne rivers were stocked in 1990 with only 14 000 and 10 000 individuals, respectively.

Sampling

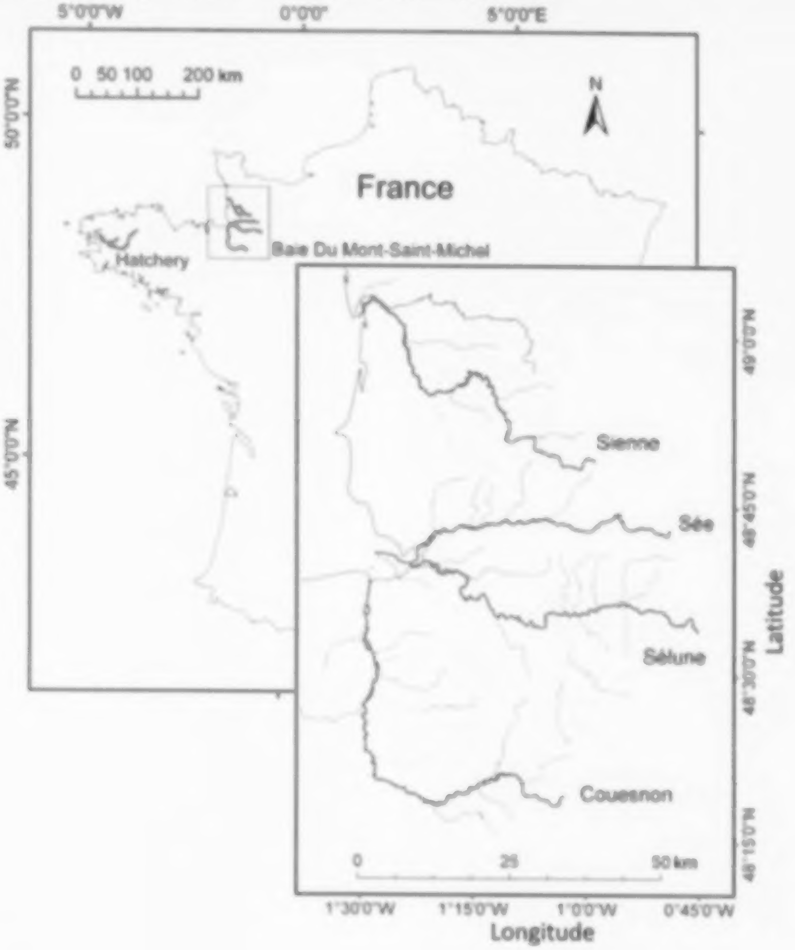
In October 2007, 84 young-of-the-year Atlantic salmon ranging from 55 to 100 mm total length (TL) were collected by electrofishing in four rivers of the Bay of Mont Saint-Michel. This survey was done before the annual restocking operation in the Couesnon River. Individuals were caught in several sites on each river catchment (three to seven) depending on the area colonized by Atlantic salmon. Six young-of-the-year individuals (70–90 mm TL) were also collected in 2007 at the Favot Hatchery. All individuals were over-anaesthetized and preserved on ice in the field, and then frozen at –20 °C on the same day. In addition, carcasses of nine adult salmon were collected after they had spawned in the vicinity of the spawning grounds in the Sélune River in January 2008. Postspawning fish were about to die or had recently died (1 or 2 d prior) when collected. Finally, scales from 25 individuals caught in the Aulne River in 2006 were also collected for genetic analyses.

Genetic analyses

DNA analyses

Genomic DNA was extracted from scales (adults) or pelvic fins (juveniles) by heating samples in 230 mL solution (proteinase K, Tris/EDTA buffer, and chelex) at 55 °C for 2 h and then at 100 °C for 10 min (Estoup et al. 1996). The M13 method (Schuelke 2000) was used to label DNA polymerase chain reaction (PCR) amplifications. DNA was amplified using six microsatellite markers (*BHMS235*, *BHMS111*, *BHMS377* (Hoyheim 2000), *SSA197*, *SSA171*, and *SSA65* (O'Reilly et al. 1996)). PCR was carried out in a 10 mL reaction volume containing 1.5 mmol/L $MgCl_2$, 200 mmol/L dNTPs, 0.1 mmol/L forward primer, 0.15 mmol/L reverse primer, 0.15 mmol/L M13-Fluo, 25–50 ng DNA, and 0.5 U *Taq* DNA polymerase. The amplification conditions were as follows: an initial denaturation for 5 min at 94 °C, 42–45 cycles for 30 s at 94 °C, 30 s at annealing temperature, 30 s at 72 °C, and a final synthesis for 30 min at 72 °C.

Fig. 1. Location of Couesnon, Sélune, Sée, and Sienne rivers in the Bay of Mont-Saint Michel (Normandy, France). These rivers have been stocked with hatchery-reared fish that originated from the Aulne River (Brittany, France).



Statistical analyses

Tests for linkage and Hardy–Weinberg disequilibrium were conducted with FSTAT 2.9.3.2 (Goudet 1995). The allelic richness (number of alleles corrected for sample size) was calculated for all loci and populations using FSTAT 2.9.3.2. The expected heterozygosity (H_E, Nei 1978) and observed heterozygosity (H_O) were calculated with GENETIX 4.05.2 (Belkhir et al. 1996). GENETIX 4.05.2 was then used to compute a two-dimensional correspondence factorial analysis (CFA). We investigated the potential genetic structure among clusters of individuals without a priori knowledge on their geographic origin using the Structure software (Pritchard et al. 2000). The number of genetic groups (k) tested was from one to five, with each run consisting of a burn-in period of 50 000 steps followed by 300 000 Markov chain Monte Carlo replicates. Geneclass (Piry et al. 2004) was also used to assign individuals to the five potential origins using a leave-one-out procedure, excluding self assignment (the Baudouin and Lebrun (2001) approach was used).

Elemental analyses

Otolith preparation

Otoliths were extracted with plastic and glass tools that were cleaned with ultrapure Milli-Q water (18 Ω) and 10% nitric acid (HNO_3) to prevent contamination. Otoliths were then cleaned in ultrapure water to remove any remaining tissues. They were finally embedded in epoxy resin and polished with diamond paste in the sagittal plane to expose the core.

Laser ablation ICPMS

A femtosecond laser ablation system (Alfamet, Novalase SA – Amplitude Systemes, Pessac, France) that was fit with a diode-pumped KGW-Yb laser source (360 fs, 1030 nm) was employed (Pecheyran et al. 2005). The laser was used at a high repetition rate (3 kHz), with a laser beam diameter of 9 μm. A galvanometric scanning beam device, which was fit between the laser source and the objective, permitted the laser beam to move rapidly (up to 280 mm/s) with a high repositioning precision (<1 µm). When operated at high repetition rates, this system allowed the ablating of a sample very rapidly according to two-dimensional trajectories as reported elsewhere (Fernández et al. 2008; Claverie et al. 2009). The laser ablation system was coupled to an Elan DRC II inductively coupled plasma mass spectrometer (ICPMS, Perkin Elmer, Waltham, Massachusetts). The optimization of gas flows (helium and argon), plasma conditions, and lens voltage was performed by ablating a SRM 612 (National Institute of Standards and Technology, Gaithersburg, Maryland) glass series, with respect to an oxide level of <3% (ThO/Th < ~3%) and U/Th ratio of 1.00 ± 0.05 to ensure optimal particle atomization and maximum signal sensitivity.

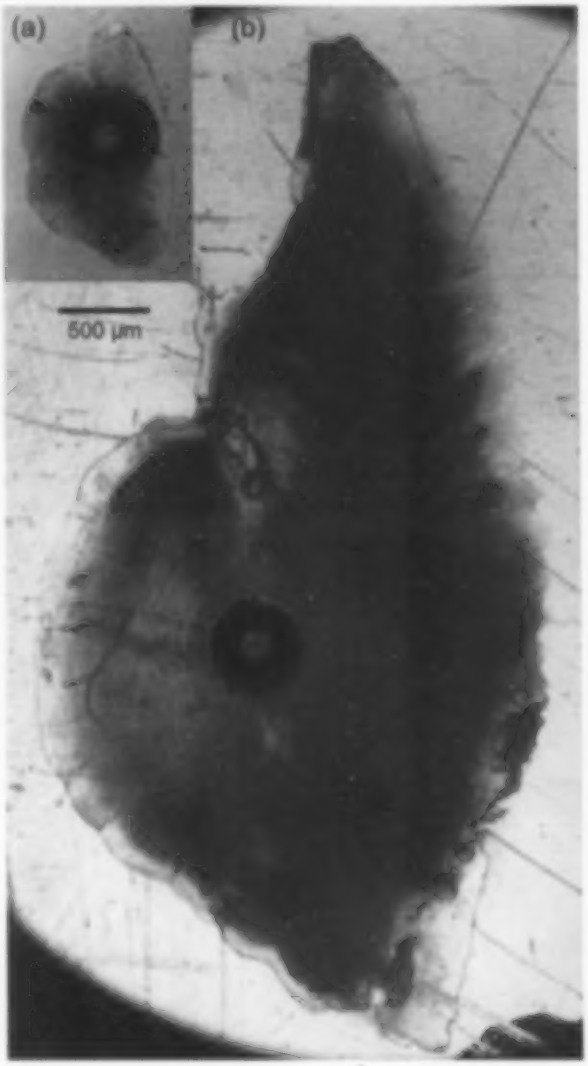
Laser ablation strategy

The ablated area corresponded to a 200–600 µm wide annulus centered on the primordium (Fig. 2). The ablation was realized using the two-dimensional scanner according to a succession of 100 concentric circles ranging in diameter from 200 to 600 µm, with the laser beam moving rapidly at 8 mm/s. This resulted in the ablation of a large amount of material (0.25 mm^2 area) in about 16 s, providing a global aerosol subsequently introduced into the ICPMS. The smallest diameter of the annulus (200 µm) was defined to fit with the largest size of otolith at the beginning of the juvenile period (exogenous feeding) according to preliminary tests and values in Metcalfe et al. (1992). The largest diameter (600 µm) corresponded to the smallest otolith found in our juvenile samples. This original laser ablation strategy (Fig. 2) was essential to (*i*) avoid nucleus material corresponding to maternal signature (Donohoe et al. 2008), (*ii*) integrate the elemental signal corresponding to the entire growing period of juveniles in freshwater and to average fluctuations that could possibly be encountered, (*iii*) increase the quantity of material analyzed and improve detection limits, and (*iv*) be able to reproduce such a design on otoliths of adults to obtain trace elemental signatures corresponding to the juvenile period only. Prior to recording the signal, the otolith area to be ablated was cleaned by preablation with a low energy laser beam (2 µJ) to soften the surface contamination that was likely to occur.

Trace element quantification

Fourteen elements (17 isotopes) of interest were recorded: ^{7}Li, ^{23}Na, ^{24,25}Mg, ^{27}Al, ^{43}Ca, ^{55}Mn, ^{59}Co, ^{63}Cu, ^{66,68}Zn, ^{85}Rb, ^{86}Sr, ^{111,113}Cd, ^{138}Ba, and ^{208}Pb, with ^{43}Ca being used as an internal standard to correct for mass removal variations due to uneven sample surfaces and ICPMS drift. Signal processing was performed using Elan Instrumental software (Perkin Elmer). A series of two calcium carbonate standards containing the coprecipitated trace elements of interest at expected concentrations ranging from 5 to 20 µg/g were prepared (Barats et al. 2007). For each calcium carbonate standard, 20 mg of the coprecipitated powder was used and pressed in a 3 mm die. The fish-otolith-certified reference material no. 22 (National Institute for Environmental Studies, Tsukuba, Japan; Yoshinaga et al. 2000) was used to assess the reliability of the $CaCO_3$ pellets and to match with the high Sr concentrations (>2000 µg/g), which were eventually found in marine fish otoliths (Daverat et al. 2005), as well as with ultra low concentrations (Zn and Cu). Trace elements in otoliths were quantified by external calibration using the enriched $CaCO_3$ pellets. Calibration was carried out at the beginning and at the end of each analytical series to compensate for ICPMS drift. Each analytical series took about 3 h. As mentioned above, a large amount of material was ablated in a short period of time, which resulted in the introduction of a large amount of thin particles into the ICPMS per time unit. This, in turn, generated a high ICPMS signal intensity and very low instrumental limits of detection at the nanogram per gram level. Instrumental limits of detection (in nanograms per gram) obtained on calcium carbonate under our operating conditions and expressed as three times the standard deviation of the carrier gas background (He)

Fig. 2. Pictures of (*a*) juvenile and (*b*) adult Atlantic salmon otoliths showing the area ablated by the laser prior to inductively coupled plasma mass spectrometry analysis. The annulus ablated is 200–600 µm, is centered on the primordium, and corresponds to the juvenile period of growth only.



were as follows: ^{7}Li, 2.8; ^{24}Mg, 12.1; ^{55}Mn, 17.4; ^{63}Cu, 4.4 ; ^{66}Zn, 61.9; ^{68}Zn, 103.6; ^{138}Ba, 1.1; ^{208}Pb, 0.8; ^{23}Na, 458.0; ^{86}Sr, 182.1; ^{111,113}Cd, 0.09. Note that to prevent overloading of the detector, ^{86}Sr and ^{23}Na signals were strongly attenuated, which explains the poor instrumental limits of detections for these elements.

Statistical analyses

Discriminant function analyses (DFA) that included 12 elements (Li, Na, Mg, Al, Mn, Co, Cu, Zn, Rb, Sr, Ba, and Pb) were used to differentiate samples from the four rivers and the hatchery. This was a stepwise analysis with forward selection. The significance of each element variation was tested with an F-statistic, and the redundancy of variables was tested by a tolerance measurement using XLStat-Pro software (xlstat.com). A jack-knifed classification matrix was used to estimate the correct assignment of individuals to their natal river.

Combination of genetic and trace element analyses

For each individual, genetic assignment scores were coupled with trace element scores. Genetic scores were the assignment proportions to the two genetic clusters detected (wild and hatchery) with the Structure software. A score close to zero indicated a hatchery pedigree, while a score close to one indicated wild pedigrees. Scores from 0.3 to 0.7 likely corresponded to hybrid pedigrees between hatchery-born and wild fish. Trace element scores were calculated from canonical coordinates on the three first axes of the DFA (hereinafter X, Y, and Z, explaining 92.5% of variance). First, the five centroids for juveniles originating from the hatchery (h) and from each river (r) were calculated as the mean value on each axis (X_h, Y_h, and Z_h for hatchery juveniles; X_r, Y_r, and Z_r for wild juveniles of each river). Then, the distance from each individual (i) to the centroid h was calculated following the equation

$$(1)\qquad D_{ih} = \sqrt[2]{(X_i - X_h)^2 + (Y_i - Y_h)^2 + (Z_i - Z_h)^2}$$

where X_i, Y_i, and Z_i are coordinates of i on X, Y, and Z axes, respectively. Similarly, the distance from each individual (i) to the centroid r of its natal river was calculated as

$$(2)\qquad D_{ir} = \sqrt[2]{(X_i - X_r)^2 + (Y_i - Y_r)^2 + (Z_i - Z_r)^2}$$

Then, the trace element score of each individual S_i was calculated as

$$(3)\qquad S_i = \frac{D_{ih}}{D_{ih} + D_{ir}}$$

Elemental trace scores close to zero or one indicated a hatchery or wild origin, respectively. The threshold score between hatchery and wild elemental trace signatures was set to 0.3, which corresponds to the maximum value observed among samples from the Favot Hatchery. For adult individuals, S_i was calculated the same way as for juveniles, choosing the statistically closest river to calculate D_{ir}. Genetic and elemental trace scores were then plotted together, allowing the classification of individuals into six groups: (*i*) river born with wild pedigree, (*ii*) river born with hybrid pedigree, (*iii*) river born with hatchery pedigree, (*iv*) hatchery reared with hatchery pedigree, (*v*) hatchery reared with hybrid pedigree, and (*vi*) hatchery reared with wild pedigree. The last two groups should theoretically contain no individuals because no fish from Normandy were used at the Favot Hatchery.

Results

Molecular analyses

Only 3 out of 42 inbreeding coefficients (F_{IS}) were significant, but they were not associated with a particular locus or population. In all populations, F_{IS} were not significant (Table 1). Average observed heterozygosities (H_O) and expected heterozygosities (H_E) were 0.80 and 0.81, respectively. Allelic richness ranged from 5.3 to 5.9. Pairwise F_{ST} were extremely low and not significant among the four Normandy populations, ranging from 0.0002 to 0.012. Conversely, pairwise F_{ST} between hatchery and Normandy samples were significant, ranging from 0.03 to 0.08 (average = 0.06). The genetics correspondence factorial analysis (CFA) confirmed the genetic proximity among the four Normandy rivers, because genotypes from these populations largely overlapped (Fig. 3*a*). This analysis also revealed clear differences between hatchery and wild individuals.

The Geneclass software correctly classified 25%–47% of juveniles collected in rivers and 100% of hatchery-reared juveniles (Table 2). Among the nine adults caught in the Sélune River, seven were assigned to Normandy populations and two were assigned to the hatchery. Similarly, the Bayesian clustering method that was implemented in Structure software did not reveal any structure among populations from Normandy but delineated two clusters corresponding to fish from the hatchery and wild populations. In juvenile hatchery samples, the admixture with the wild cluster was low (0.09). In contrast, wild populations were significantly admixed with the hatchery cluster, with values of 0.45, 0.32, 0.18, and 0.22 in the Couesnon, Sélune, Sée, and Sienne rivers, respectively. Eleven juveniles (12%) caught in Normandy rivers clustered with hatchery samples and were considered as offspring of individuals that originated from the hatchery. Thirteen juveniles (14%) showed intermediate scores (from 0.31 to 0.69) and were considered as hybrid progenies of hatchery and wild adults. The remaining 69 juveniles (74%) collected in Normandy rivers clustered with native populations. The results obtained with Geneclass and Structure were mostly concordant; among the 15 juveniles assigned to the hatchery by Geneclass, Structure detected 11 individuals that originated from the hatchery and 4 hybrids. The nine remaining hybrids found by Structure were assigned to wild populations by Geneclass. Finally, two adults clustered with hatchery samples, three were hybrids, and four clustered with wild populations.

Elemental analyses

Concentrations of Cd in otolith samples were extremely low and usually below the detectable limit. Therefore, this element was not considered in subsequent data analyses. We detected significant differences among sites in otolith elemental concentrations of Li, Mg, Mn, Ba, Sr, and Rb but not for Al, Cu, Zn, Pb, Na, and Co (Table 3). Mg concentrations were particularly high in the hatchery otoliths. The four

Table 1. Within-population estimates of genetic diversity.

Location	Life stage	*n*	F_{IS}	H_E	H_O	R_A
Couesnon	Young-of-the-year	12	–0.03	0.78	0.81	5.8
Sélune	Young-of-the-year	25	–0.06	0.80	0.85	5.7
Sée	Young-of-the-year	32	–0.06	0.77	0.80	5.3
Sienne	Young-of-the-year	15	–0.01	0.79	0.80	5.4
Hatchery	Young-of-the-year	6	0.07	0.77	0.72	5.3
Sélune	Adult	9	0.04	0.82	0.80	5.9
Hatchery	Adult	25	–0.01	0.81	0.82	5.9

Note: Sample size (*n*), inbreeding coefficient (F_{IS}), expected heterozygosity (H_E), observed heterozygosity (H_O), and average allelic richness (R_A) per locus for six individuals are given.

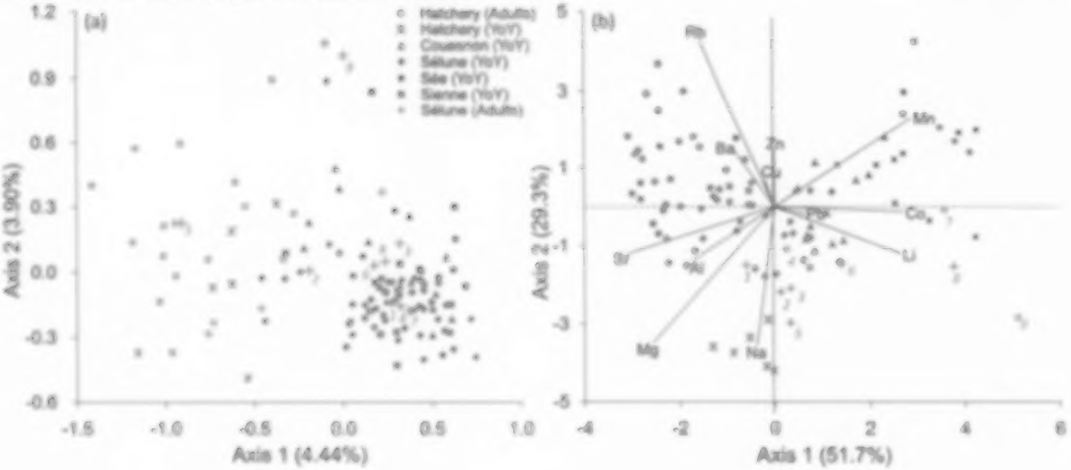


Fig. 3. (*a*) Correspondence factorial analysis of all genotypes analysed and (*b*) discriminant function analysis (DFA) of otolith elemental concentrations for individuals collected in Couesnon, Sélune, Sée, and Sienne rivers and at the hatchery. Adults collected on the Sélune River after spawning are labeled 1–9. Note that the three first axes of the DFA were used for individual assignment to the source populations (Table 2), but only two axes are displayed for a convenient reading.

rivers and the hatchery were well distinguished by the DFA (Fig. 3*b*). Most juveniles (83%–100%) were correctly assigned to their natal origin: river or hatchery (Table 2). Five out of nine adults were assigned to the Sélune River where they were caught, three were assigned to the Sienne River, and one was assigned to the hatchery.

Coupling genetic and microchemistry

Juvenile otolith elemental concentrations and microsatellite analyses confirmed that hatchery-reared juveniles displayed specific genetic and trace element signatures from the hatchery (Fig. 4). All juveniles collected in Normandy rivers were born in these rivers, but molecular analyses revealed multiple genetic origins: wild, hatchery, or hybrids. For adult salmon carcasses collected on the Sélune River after spawning, elemental and molecular signatures suggested multiple geographic and genetic origins. Adults 5 and 2 had hatchery pedigrees; elemental analysis revealed that they were born in the hatchery and the Sélune River, respectively. Adults 3 and 6 were hybrids born in the Sélune River, whereas adult 9 was a hybrid born in the Sienne River. Finally, the four adults with wild pedigrees were born in the Sélune (adults 1 and 4) and Sienne rivers (adults 7 and 8).

Discussion

In this study, otolith trace element and genetic analyses were combined to explore the origin of Atlantic salmon in four adjacent rivers of the Bay of Mont Saint-Michel. Microsatellite analyses confirmed the low level of genetic differentiation among these rivers observed by Grandjean et al. (2009). The assignment of wild individuals to their natal river based on molecular data was impossible, certainly because of the low differentiation among populations (Faubet et al. 2007). Other cases of weak differentiation among Atlantic salmon populations living in adjacent river catchments have been previously reported and attributed to high gene flow between nearby stocks (Dionne et al. 2009).

The genetic differentiation between hatchery-reared and wild individuals was significant enough to track hatchery pedigrees in wild populations. The Couesnon and Sélune rivers have been intensively stocked over past decades with salmon originating from Brittany. Accordingly, a large proportion of juveniles collected in Normandy rivers have complete or partial hatchery pedigrees. This result confirms the successful reproduction of some hatchery-reared Atlantic salmon after their release in Normandy rivers. Other studies already reported the presence of hybrids between wild and

Table 2. Individual assignment to the population of origin using genetic and elemental data.

Location	Life stage	Sample size	Assignment using genetic data						Assignment using elemental data					
			Couesnon	Sélune	Sée	Sienne	Hatchery	Correct	Couesnon	Sélune	Sée	Sienne	Hatchery	Correct
Couesnon	Young-of-the-year	12	3	1	2	1	5	25%	10	1	0	1	0	83%
Sélune	Young-of-the-year	25	2	8	6	3	6	32%	1	21	3	0	0	84%
Sée	Young-of-the-year	32	3	8	15	5	1	47%	0	0	32	0	0	100%
Sienne	Young-of-the-year	15	1	2	4	5	3	33%	2	0	0	13	0	87%
Hatchery	Young-of-the-year	6	0	0	0	0	6	100%	0	0	0	0	6	100%
Sélune	Adult	9	1	3	2	1	2	—	0	5	0	3	1	—
Hatchery*	Adult	25	0	0	1	0	24	—	—	—	—	—	—	—

Note: In contrast with juveniles collected in their natal rivers and at the hatchery, the true natal origin of adults was unknown, so the estimation of the proportion of correct assignment was not possible for these individuals.

*Adults used at the hatchery are collected yearly in the Aulne River (in Brittany). Because of their high conservation value, they were released just after artificial fecundation, and only scale tissue was sampled on each individual. No trace element analyses on otoliths are available.

hatchery fish in stocked populations (Hansen 2002; Finnegan and Stevens 2008; Hansen et al. 2009). We found that 14% of the juveniles collected in Normandy rivers were such hybrids. However, juveniles with pure wild pedigrees were also collected, indicating indigenous salmon persistence in such introgressed populations, as observed in brown trout *Salmo trutta* by Hansen and Mensberg (2009). Conversely, young-of-the-year juveniles with pure hatchery pedigrees were detected in all rivers and before annual restocking operation in the Couesnon River, which strongly suggests the presence of breeding between hatchery-reared individuals on natural redds.

Unlike DNA, the geochemical signature of otoliths is, for the most part, not inherited from parents (except a maternal signature in otolith primordium) but, rather, depends on the environment in which the organism lives. Since otoliths integrate ambient water elements during fish growth, it was possible to discriminate river-born and hatchery-born juveniles owing to trace elements incorporated in the portion of otoliths corresponding to juvenile growth. Recent studies based on isotopic and elemental analyses reported similar findings (Sohn et al. 2005; Gao and Bean 2008; Gibson-Reinemer et al. 2009). Elemental concentrations of Ba, Li, Mn, Rb, and Sr in juvenile otoliths significantly discriminated the four natal rivers. These elements are not strongly involved in physiological processes, which suggests that their concentrations in otoliths are mostly linked to the composition of the ambient water. These elements have already been pointed out as appropriate tracers in Allis shad (*Alosa alosa*; Tomas et al. 2005) and gray snapper (*Lutjanus griseus*; Thorrold et al. 1997; Tomas et al. 2005; Lara et al. 2007). We also detected significant differences in elemental concentrations between individuals originating from the hatchery and Normandy rivers; such differences may be explained by variations in water chemistry but also by variations in water temperature during growth (Mitsuguchi et al. 1996).

By identifying fish pedigrees and the environment where they grew as juveniles, joint genetic and trace element analyses provide new cues to study the life histories and origins of Atlantic salmon living in Normandy rivers. Several studies used individual admixture analyses based on multilocus data to discriminate wild, stocked, and hybrid fish (Hansen 2002; Hansen and Mensberg 2009). However, using molecular data only, it is impossible to certify the origin of individuals with hatchery genetic characteristics. Such individuals may indeed originate from the hatchery or be the progeny of hatchery-reared fish having bred together in nature.

Atlantic salmon has a high conservation value in the Bay of Mont Saint-Michel, making the lethal sampling of otoliths on adults returning to freshwater spawning grounds not feasible. We only found nine carcasses of adult salmons in the vicinity of spawning grounds in the Sélune River, despite substantial efforts in winter 2007 and winter 2008. However, these nine adult samples were very informative, since it was possible to infer their natal origin owing to the laser ablation of their otoliths. The region ablated on an adult's otolith covers the juvenile period of growth. The resulting elemental signatures were then compared with reference signatures obtained by similar laser ablations on otoliths of juveniles of known origins. These nine adults were successfully assigned to their geographic origin. However, Fig. 3*b* suggests that

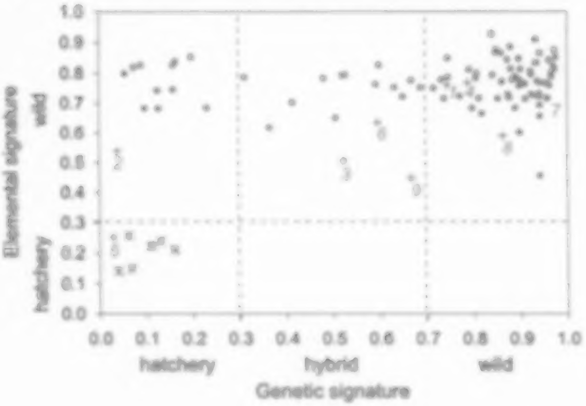
Table 3. Spatial variability of 12 elements measured in juvenile Atlantic salmons collected in four Normandy rivers and at the Favot Hatchery.

	Concentrations for each study site					
Element	Couesnon	Sélune	Sée	Sienne	Hatchery	p
Li	0.02±0.00	0.02±0.00	0.01±0.00	0.05±0.01	0.04±0.00	< 0.0001
Na	3815.16±86.76	3813.88±108.88	3764.62±147.52	3669.31±110.26	3496.46±253.58	ns
Mg	15.28±2.06	12.96±1.52	18.27±7.33	13.20±1.77	45.39±22.07	< 0.0001
Al	0.25±0.13	0.43±0.26	0.41±0.21	0.57±0.30	0.34±0.23	ns
Mn	7.33±1.51	5.23±1.23	4.49±0.88	12.56±1.62	2.81±0.49	< 0.0001
Co*	0.97±0.02	0.95±0.02	0.95±0.02	0.97±0.02	0.93±0.02	ns
Cu	0.11±0.02	0.10±0.02	0.18±0.17	0.13±0.05	0.08±0.01	ns
Zn	54.53±2.71	52.58±4.03	52.02±6.18	49.44±3.78	54.13±10.03	ns
Rb*	11.65±2.28	12.15±2.15	20.78±3.95	17.23±4.34	6.29±1.37	< 0.0001
Sr	632.38±34.11	766.18±47.22	837.07±41.96	604.74±33.36	759.44±75.78	< 0.0001
Ba	11.27±0.66	12.60±2.39	16.45±1.69	10.16±1.09	7.81±1.01	< 0.0001
Pb	0.03±0.02	0.02±0.01	0.04±0.03	0.25±0.36	0.16±0.19	ns

Note: Mean values ± SD in micrograms per gram are given for each element in each site. Results from ANOVAs testing potential differences among sites are presented.

*Values normalized against CRM NIES 22 $R =$ [illegible], where M is Rb or Co.

Fig. 4. Dual plot of trace element and genetic scores for each fish analyzed in this study. Trace element scores were computed from the discriminant function analysis and genetic scores with the Structure software (see text for details). Juveniles were collected in Normandy rivers (●) and at the Favot Hatchery (⌘); adults were collected on the Sélune River (+) after spawning and are labeled 1–9.



some adult elemental fingerprints were slightly different from any of the source populations. We cannot exclude the hypothesis that some adults recaptured in the Sélune River could have come from unsampled reference groups. Another possible explanation is that interannual modifications of local water chemistry, and consequently in elemental otolith fingerprints, could have occurred (Campana et al. 2000; Swearer et al. 2003; Gillanders 2005). Therefore, because adults did not belong to the same cohort as juveniles, this could have confused their elemental assignment. Nevertheless, four of the nine adults were clearly identified as offspring of wild fish since they had both genetic and elemental signatures of wild juveniles. They were most probably born in the Sélune and Sienne Rivers and reproduced in the Sélune River where carcasses were found. Conversely, one adult was born in the hatchery, since it had a hatchery pedigree and an elemental signature of the hatchery in its otolith. Scale reading revealed that this fish was 3 years old. After being stocked in autumn 2005 in the Couesnon River, it migrated to the sea and returned to the Sélune River to spawn in winter 2007–2008. Three adults likely resulted from the interbreeding in nature between wild fish and individuals with hatchery pedigrees. Elemental analyses suggested that these individuals were born in the Sélune and Sienne Rivers and then reproduced and died in the Sélune River. Finally, one adult with a pure hatchery pedigree likely resulted from the natural reproduction of two adults with a similar pedigree in the Sélune River since its otolith revealed an elemental signature of this river during the juvenile period. Overall, these results reveal an important straying of both hatchery-reared and wild adult salmons as previously suggested in several studies (Stabell 1984; Quinn 1993; Jonsson et al. 2003).

In conclusion, we detected significant differences in otolith trace element concentrations of juvenile Atlantic salmon from Normandy rivers, while no genetic differentiation was observed among these populations. Using elemental traces in otoliths, more than 80% of juveniles collected in the wild were accurately assigned to their natal river. We also found trace element and genetic differences between wild and hatchery stocks allowing the assignment of individuals to these two groups and demonstrating the hybridization between fish with hatchery pedigrees and wild individuals. This joint approach of elemental and genetic analyses also revealed that individuals with hatchery pedigrees can breed together in the wild. Their offspring consist of river-born juveniles with pure hatchery pedigrees that can be mistaken for hatchery-raised and released juveniles. Overall, this study suggests that combining otolith trace element and genetic analyses on the same individuals could provide new insights into the introgression processes at work in wild populations stocked with hatchery fish. Furthermore, it could be helpful for studying colonization or recolonization processes in depopulated rivers.

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Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA

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Abstract: Recent and projected climate warming trends have prompted interest in impacts on coldwater fishes. We examined the role of climate (temperature and flow regime) relative to geomorphology and land use in determining the observed distributions of three trout species in the interior Columbia River Basin, USA. We considered two native species, cutthroat trout (*Oncorhynchus clarkii*) and bull trout (*Salvelinus confluentus*), as well as nonnative brook trout (*Salvelinus fontinalis*). We also examined the response of the native species to the presence of brook trout. Analyses were conducted using multilevel logistic regression applied to a geographically broad database of 4165 fish surveys. The results indicated that bull trout distributions were strongly related to climatic factors, and more weakly related to the presence of brook trout and geomorphic variables. Cutthroat trout distributions were weakly related to climate but strongly related to the presence of brook trout. Brook trout distributions were related to both climate and geomorphic variables, including proximity to unconfined valley bottoms. We conclude that brook trout and bull trout are likely to be adversely affected by climate warming, whereas cutthroat trout may be less sensitive. The results illustrate the importance of considering species interactions and flow regime alongside temperature in understanding climate effects on fish.

Résumé : Les tendances récentes et prévues de réchauffement du climat ont suscité de l'intérêt pour les impacts sur les poissons d'eau froide. Nous examinons le rôle du climat (température et régime hydraulique) en fonction de la géomorphologie et de l'utilisation des terres dans la détermination de la répartition observée chez trois espèces de « truites » dans le bassin versant intérieur du Columbia, É.-U. Nous observons deux espèces indigènes, la truite fardée (*Oncorhynchus clarkii*) et l'omble à tête plate (*Salvelinus confluentus*), ainsi que l'omble de fontaine (*Salvelinus fontinalis*) non indigène. Nous étudions aussi la réaction des espèces indigènes à la présence de l'omble de fontaine. Les analyses consistent en des régressions logistiques à niveaux multiples sur une base de données de grande envergure géographique de 4165 inventaires de poissons. Les résultats indiquent que les répartitions des ombles à tête plate sont fortement reliées aux facteurs climatiques et moins fortement corrélées à la présence d'ombles de fontaine et aux variables géomorphologiques. Les répartitions des truites fardées sont faiblement reliées au climat, mais fortement reliées à la présence de l'omble de fontaine. Les répartitions des ombles de fontaine sont reliées à la fois au climat et aux variables géomorphologiques, en particulier la proximité des fonds de vallées élargis. Nous concluons que l'omble de fontaine et l'omble à tête plate seront vraisemblablement affectés négativement par le réchauffement climatique, alors que la truite fardée sera peut-être moins sensible. Nos résultats soulignent l'importance de considérer les interactions entre les espèces et le régime hydraulique en plus de la température pour comprendre les effets du climat sur les poissons.

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Introduction

Recent warming trends and projections of future climate change have prompted interest in the climate sensitivity of aquatic organisms (Parmesan 2006; Battin et al. 2007; McCullough et al. 2009). Climate sensitivity (i.e., a species' sensitivity to climate change) can differ even among closely related species (Jonsson and Jonsson 2009) and be influenced by other factors that govern species distribution and abundance. These include relatively immutable features related to basin geomorphology, as well as human activities such as land use. These variables may act independently or interact with climate impacts (e.g., the mediation of temperature and flow changes by groundwater; Power et al. 1999; Tague et al. 2008). Climate change is also expected to significantly alter invasive species distributions (Rahel and Olden 2008). Therefore, an assessment of climate sensitivity should consider both the range of direct effects on the species of concern as well as potential indirect effects resulting from changes in the distributions of invasive species (Poloczanska et al. 2008; Bradley 2009).

Trout, char, and salmon (hereinafter collectively referred to as trout) are of particular interest because of their economic importance, their need for cold water, and the imperiled status of many species. Past studies of climate influences on trout focused primarily on temperature or surrogates of temperature (Keleher and Rahel 1996; Rieman et al. 2007; Kennedy et al. 2009). This is reasonable because all climate projections agree that global temperatures will increase (IPCC 2007), potentially causing trout distributions to shift to higher latitudes and elevations (Jonsson and Jonsson 2009; Rieman and Isaak 2010). Some studies have also examined the role of climate-driven shifts of hydrologic regimes, particularly extreme flows (Jager et al. 1999; Battin et al. 2007). An example of such a hydrologic relationship is the sensitivity of trout eggs and fry to high flows. Evidence suggests that high flows in the post-spawning period can reduce recruitment (Seegrist and Gard 1972; Latterell et al. 1998; Warren et al. 2009) and limit species distributions (Fausch et al. 2001; Fausch 2008). In regions that receive precipitation mainly as snow in winter, the frequency of high winter flows is temperature-dependent and may increase in a warming climate (Hamlet and Lettenmaier 2007; Barnett et al. 2008). These changes may lead to increased bedload movement in streams, causing mortality of eggs and alevins for fall-spawning species such as brook trout (*Salvelinus fontinalis*) and bull trout (*Salvelinus confluentus*; Shellberg et al. 2010). Such changes may depend on landscape topography, since many fall-spawning species use unconfined valley bottoms (UVBs) for spawning (Baxter and Hauer 2000; Dunham et al. 2002; Benjamin et al. 2007), and these locations may provide velocity refugia at high flows (Shellberg et al. 2010). Other landscape and anthropogenic variables that may be of fundamental importance in determining trout distributions include stream size and slope (Lanka et al. 1987; Rahel and Nibbelink 1999; Isaak and Hubert 2000) and human activities such as logging and road construction (e.g., Dunham and Rieman 1999; Trombulak and Frissell 2000; Shepard et al. 2005).

Nonnative species pose another major threat to trout. In the western US, the brook trout is an invasive species that can displace native trout (Thurow et al. 1997; Dunham et al. 2002; Peterson et al. 2004*a*). In some locations, brook trout invasions have been so successful that native species such as cutthroat trout (*Oncorhynchus clarkii*) persist only above artificial barriers maintained to exclude invasives (Fausch et al. 2009). However, the fall-spawning brook trout may be more sensitive to a climate-associated increase in winter flooding than the spring-spawning cutthroat trout. This raises the possibility of cascading climate effects, and suggests that an analysis of the climate sensitivity of native species such as cutthroat trout should include consideration of the climate sensitivity of nonnative species such as brook trout.

In this study we assessed the relative roles of climate (temperature and flow), geomorphology (valley bottom confinement, slope, and stream size), road proximity, and species interactions in structuring the current spatial distributions of nonnative brook trout and native cutthroat and bull trout. Our study area was the US portion of the interior Columbia River Basin. Our analysis was facilitated by the recent development of a database of modeled stream flows at the reach scale (Wenger et al. 2010) and the compilation of an exceptionally large fish collection dataset.

Materials and methods

Study area and organisms

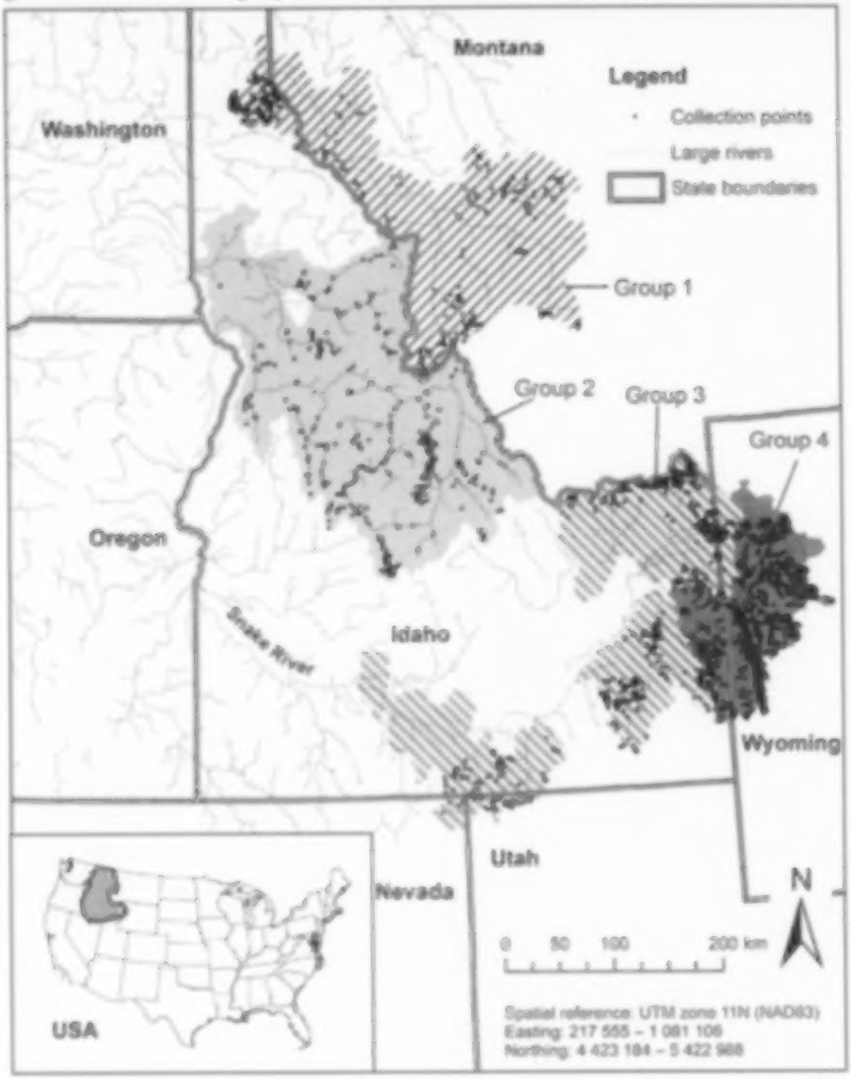
The US portion of the interior Columbia River Basin (ICRB) lies within the northern Rocky Mountains and intermountain regions of the northwestern United States (Fig. 1). The southern part of the basin is relatively dry, with most precipitation falling as snow in winter at high elevations, producing snowmelt-dominated flow regimes. The northern part of the basin is more mesic and receives a greater proportion of precipitation as rain, but still tends to be snow-dominated. Elevations range from ~500 to ~3500 m a.s.l. More detailed descriptions of climate and vegetation of the ICRB are available elsewhere (Quigley et al. 1996).

Trout that are native to at least a portion of the ICRB include bull trout, rainbow trout (*O. mykiss*), and cutthroat trout (Thurow et al. 1997). Cutthroat trout in the ICRB are separated into two subspecies: westslope (*O. c. lewisi*), and Yellowstone (*O. c. bouvieri*). The bull trout is listed as a threatened species under the US Endangered Species Act (ESA). The cutthroat trout is a species of conservation interest to state and federal management agencies, although none of the subspecies in the ICRB are currently listed under the ESA. Nonnative and potentially invasive trout introduced into the region include brook trout, brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and hatchery-origin rainbow trout. All are considered threats to native trout (Thurow et al. 1997), but the ecological displacement of native species by brook trout has been a particular concern (Dunham et al. 2002; Peterson et al. 2004*a*; Rieman et al. 2006). In some instances, brook trout may also hybridize with bull trout, although introgression is often limited (Kanda et al. 2002; DeHaan et al. 2010).

Data and hypotheses

We developed 10 hypotheses to explain the expected relationships between trout distributions and predictor variables in the ICRB (Tables 1 and 2). The hypothesized relationships

Fig. 1. Map of study area, collection sites, and validation groups in the Columbia River Basin (inset map shows location in the northwestern USA). Sites were assigned to the four validation groups based on spatial location for purposes of cross-validating model performance.


Montana
Legend
Collection points
Large rivers
State boundaries
Washington
Group 1
Group 2
Group 3
Group 4
Oregon
Idaho
Snake River
Wyoming
Utah
Nevada
USA
N
0 50 100 200 km
Spatial reference: UTM zone 11N (NAD83)
Easting: 217 555 – 1 081 106
Northing: 4 423 184 – 5 422 988

were organized into groups of climate, geomorphic, biotic, and land-use predictors, as well as two potential interactions. Below we describe the fish distribution dataset, hypotheses, and methods of quantifying the predictor variables used in hypothesis tests.

Fish occurrence database

The fish occurrence database (Fig. 1) was assembled from fish data collections made by the Idaho Fish and Game Department; Montana Fish, Wildlife and Parks; the Wyoming Game and Fish Department; and the US Forest Service. The original data collection efforts included inventories, monitoring, and research conducted from 1985 to 2004. In assembling this database, we included only sites within the historical range of cutthroat trout sampled using electrofishing or snorkeling. Because detection by snorkeling can be less efficient than electrofishing (Thurow et al. 2006), snorkeling sites with fewer than four repeat visits were excluded from the dataset. We also excluded sites within basins with drainage areas larger than 400 km^2 because our method for estimating flows was not intended for large rivers (Wenger et al. 2010) and species detection probability could be lower in large streams (Thurow et al. 2006). Data from collections on the same stream within 50 m of one another were considered to be from the same location and treated as a single site. The final dataset included 4165 sites, of which only 339 were sampled by snorkeling. Cutthroat trout were detected at 2950 sites, brook trout at 1259 sites, and bull trout at 396 sites. For this analysis, samples were assumed to be contemporaneous, i.e., we coded a fish species as present at a site if at least one individual (adult or juvenile) was encountered at the site, regardless of date of collection. We restricted the analysis of

Table 1. Hypothesized responses of brook trout, bull trout, and cutthroat trout to candidate predictor variables that may explain fish distributions.

			Hypothesized response		
Category	Variable	Metrics	Brook trout	Bull trout	Cutthroat trout
Climate	Air temperature	ptemp, dtemp	+/– or –	+/– or –	+/– or –
	Winter high flow	w2, w1.5, w99, w95	–	–	0 or +
Geomorphic	Stream slope	slope	–	–	–
	Unconfined valley bottom	vbpres	+	+	+ or –
		vbdist	–	–	+ or –
	Stream size	mflow, sflow	– or +/–	0 or +/–	0 or +/–
Land use	Road presence	road	+	–	–
Invasive species	Brook trout in site	brk1, brk2	NA	–	–
	Brook trout in subwatershed	brkw	NA	–	–
Interactions	Winter high flow by valley bottom	[multiple combinations possible]	+	+	0
	Brook trout in subwatershed by valley bottom	brkw×vbdist or brkw×vbpres	NA	–	–

Note: A "+" indicates a positive relationship, a "–" indicates a negative relationships, and "+/–" means a unimodal relationship. Metrics are defined and described in Table 2.

bull trout to the subset of sites within its historical range, which excluded samples in the upper Snake River Basin above Shoshone Falls.

Climate hypotheses

We considered two hypotheses regarding the effects of climate on trout (Table 1). First, we hypothesized that each species would be less likely to occur in locations with temperatures outside its thermal optimum, which would produce a unimodal relationship between temperature and occurrence. Among the three trout species evaluated, we expected bull trout to require the coldest temperatures (Selong et al. 2001; Dunham et al. 2003). Second, we hypothesized that more frequent winter high flows would be detrimental to fall-spawning brook and bull trout, but not to spring-spawning cutthroat trout. We describe the flow data first because the temperature data were derived from the flow modeling process.

We calculated metrics representing winter high-flow frequency at each site using output from the variable infiltration capacity (VIC) macro-scale hydrologic model (Liang et al. 1994; 1996) run for the Pacific Northwest by the Climate Impacts Group at the University of Washington (Seattle, Wash.; Matheussen et al. 2000; Elsner et al. 2010). The VIC model is a distributed, largely physically based model that balances surface energy and water fluxes. It has been widely used in the western US to study past and potential future changes to water flow regimes (e.g., Hamlet et al. 2009), snowpacks (Hamlet et al. 2005), and droughts (Luo and Wood 2007). The implementation we used was run at the 1/16th degree scale (~7 km × ~5 km). We used a recently developed simplified routing method (Wenger et al. 2010) to apply VIC output to stream segments in the National Hydrography Dataset Plus (NHD Plus 2006) in US Geological Survey hydrologic region 17 (the Pacific Northwest). Previous model validations (Wenger et al. 2010) had demonstrated that metrics representing frequency of winter high flows were predicted with low bias and error. We calculated four metrics: w2, w1.5, w99, and w95. The first two measured the probability of a 2-year or 1.5-year recurrence interval flow event (respectively) during the winter. Flows of this magnitude are sufficiently large to mobilize bed material, potentially damaging redds and crushing embryos or alevins (Montgomery et al. 1996; Tonina et al. 2008). The latter two metrics, w99 and w95, were the number of days during winter that were among the highest 1% and 5% (respectively) of flows for the year. These were assumed to be flows with velocity sufficient to displace and kill newly emerged fry (Fausch et al. 2001), but not necessarily destroy embryos in redds. Winter was defined as 1 December – 28 February. The timing of emergence could vary widely within our study region, based on a variety of influences (e.g., Coleman and Fausch 2007), but we did not attempt to capture local variability in this analysis. All metrics were calculated across the 20 water-years from 1978 to 1997, which coincide with or slightly precede the fish collections, under the logic that flows during this period influenced the observed fish distributions.

Because stream temperature data were not available for many fish sample sites, we used air temperature as a surrogate (Keleher and Rahel 1996; Rieman et al. 2007; Williams et al. 2009), even though correlations between air temperature and water temperature are variable and sometimes weak (Isaak et al. 2010). We calculated three air temperature metrics: mean summer temperature, maximum summer temperature, and maximum weekly maximum temperature, all based on the 48-day period between 15 July and 31 August, and averaged across the 20-year period used to calculate the flow metrics described above. The three air temperature metrics were highly correlated ($r > 0.98$), so we selected mean summer temperature as a representative air temperature metric. We selected the mean because previous analyses showed a stronger air–water temperature correlation for this metric than for metrics related to maxima (Isaak et al. 2010).

For consistency we based mean summer air temperatures on the same gridded temperature values used to force the VIC hydrologic model; these in turn were derived from weather station data using empirical statistical relationships (Hamlet and Lettenmaier 2005). Air temperature data were available as a single value for the centroid of each 1/16th degree grid cell across the ICRB. Because of large elevation variability within cells, owing to complex mountain topography, we derived site-specific temperature values based on the difference in elevation between individual sites and the mean elevation of their corresponding cells, calculated from 30-m digital elevation models (DEMs; distributed as part of the NHD-plus dataset). We used an elevation adjustment value or "lapse rate" of –6.0 °C·km^{-1} derived for the ICRB by Rieman et al. (2007); this value is roughly similar to those derived for the entire Columbia River Basin (Dodson and Marks 1997) and the Alps (Rolland 2003). For each site we calculated mean summer temperature at the collection site (ptemp, for point temperature) and mean summer temperature averaged across the watershed that drains to the stream segment in which the site was located (dtemp, for drainage temperature). We assumed that this latter measurement would be better correlated with the stream temperature at each site, which is influenced by upstream temperatures (Isaak and Hubert 2001; Isaak et al. 2010).

Geomorphic hypotheses

We developed hypotheses about three predictor variables related to the geomorphic context of the stream (Table 1). First, we hypothesized that brook trout and bull trout would be more likely to occur in or near UVBs (Cavallo 1997; Baxter and Hauer 2000; Benjamin et al. 2007). We hypothesized that cutthroat trout relationships with UVBs could either be positive, if these contain favored habitats, or negative, if brook trout displace cutthroat trout from such locations (Cavallo 1997). We included an interaction term in our models to test this (see below). Second, high stream slopes could be associated with the upstream distribution limits of trout, owing to an increasing prevalence of dispersal barriers in steep channels (e.g., Fausch 1989; Dunham et al. 1999; Dunham et al. 2002). Accordingly we predicted that all three species would respond negatively to increasing stream slopes. Third, we hypothesized that brook trout, which tend to use smaller streams over large rivers (Rahel and Nibbelink 1999; Dunham et al. 2002; Öhlund et al. 2008), would show a negative or unimodal relationship with stream size. We hypothesized that bull and cutthroat trout would either show little association with stream size or a unimodal relationship driven by lower probability of their being present in the smallest and largest streams (Thurow et al. 1997).

We used an empirically derived algorithm implemented in a geographic information system (GIS), based on 30-m DEMs, to identify UVBs as relatively flat, wide valleys along streams (Nagel 2009). Valley bottoms were delineated using ground slope and convolution filtering methods. The algorithm was field validated and found to distinguish unconfined and confined valleys successfully; the former had field-measured widths of 60–500 m and a mean valley-width/channel-width ratio of 17.09, whereas the latter had widths of 5–30 m and a mean valley-width/channel-width ratio of 2.11 (n = 60; see RMRS 2010). We calculated two metrics from the valley confinement results: a binary classification of whether or not a site was in a UVB (vbpres), and distance to the nearest UVB in kilometres (vbdist).

For stream slope, we used values included in the NHD-plus dataset, which were derived for stream segments from 30-m DEMs. For stream size we used mean annual flow (mflow) and mean summer flow (sflow; summer period defined as above) from the VIC-modeled flow dataset described previously. We used flow rather than drainage area because of considerable spatial variation in precipitation across the study area. Because of this, it would have been reasonable to place this variable in the climate category rather than the geomorphic category; we chose the latter because most of the site-to-site variability in mean flow was due to watershed contributing area.

Land use hypothesis

We hypothesized that native trout species were less likely to occur in regions where there are roads near the streams (road; Table 1) because roads may reduce habitat quality and connectivity and facilitate introductions of nonnative species (Trombulak and Frissell 2000). In contrast, we hypothesized that nonnative brook trout would show a positive relationship with roads, owing to the greater probability of introductions (legal or illegal) of this species in locations accessible by road (Paul and Post 2001). The road variable was calculated as a value of 1 if the 2000 TIGER/Line road database (US Census Bureau 2002) indicated a road within 1 km of the stream segment on which the site was located, and 0 otherwise. We used this indicator of road influence, rather than road density (Rieman et al. 1997; Thurow et al. 1997; Dunham and Rieman 1999) because we were more interested in exploring site-specific impacts of roads (species introductions, angling) as opposed to impacts of roads on more diffuse watershed processes (e.g., geomorphic and hydrological impacts; Trombulak and Frissell 2000).

Invasive species hypotheses

We hypothesized that bull trout and cutthroat trout would show a negative relationship with brook trout occurrence at the scales of the site and subwatershed (40–160 km^2 based on the 12-digit NRCS hydrologic unit code; NRCS 2009). We used two candidate metrics for brook trout occurrence at the site scale: (*i*) all sites with any brook trout records (brk1, 1259 occurrences), and (*ii*) a subset of brk1 that excluded sites in which brook trout were present in <50% of samples, for those sites with multiple samples (brk2, 1143 occurrences). We calculated one subwatershed-scale metric (brkw), in which all subwatersheds with at least one brook trout occurrence were assigned the value of 1, and all other subwatersheds were assigned a value of 0.

Interactions

We considered two interactions (Table 1). First, we tested the hypothesis that UVBs provided high-flow refugia (Shellberg et al. 2010) by adding an interaction between UVBs and winter high flows, hypothesizing that response to winter high flows would be less strong within a UVB than outside of a UVB. Second, we tested the hypothesis that when brook trout were present in a watershed, they would exclude cutthroat trout and bull trout from UVBs (Cavallo 1997). We

Table 2. Descriptive statistics of metrics used as predictor variables in analyses of cutthroat trout, bull trout, and brook trout distribution in the Interior Columbia River Basin.

Metric	Abbrev.	Category	Description	Units	Range	Mean
Mean summer air temp. at point	ptemp	Climate	Mean summer temperature (15 July – 31 August) at the collection point	C	10.76–23.21	16.13
Mean summer air temp. in drainage	dtemp	Climate	Mean summer temperature (15 July – 31 August) averaged across the upstream subwatershed	C	11.15–21.63	15.96
Winter high flow 2y	w2	Climate	Probability of a 2-year recurrence interval flow in winter	Prob.	0–0.60	0.094
Winter high flow 1.5y	w1.5	Climate	Probability of a 1.5-year recurrence interval flow in winter	Prob.	0–2.00	0.166
Winter high flow 99%	w99	Climate	Number of high-flow days (top 1% of annual flows) in winter	Freq.	0–2.50	0.254
Winter high flow 95%	w95	Climate	Number of high-flow days (top 5% of annual flows) in winter	Freq.	0–8.40	0.884
Stream slope	slope	Geomorphic	Slope/gradient of the stream segment, from NHD-plus	Elev. · $dist^{-1}$	0–0.261	0.045
UVB (binary)	vbpres	Geomorphic	Within or outside of an unconfined valley bottom	—	0–1	0.247
UVB distance	vbdist	Geomorphic	Kilometres from the nearest unconfined valley bottom (UVB)	km	0–31	4.78
Mean summer flow	sflow	Geomorphic	Mean daily flow, calculated during summer months	$ft^3 \cdot s^{-1}$	0–544	12.33
Mean annual flow	mflow	Geomorphic	Mean daily flow, calculated for all months	$ft^3 \cdot s^{-1}$	0–1716	26.88
Road presence (binary)	road	Land Use	Presence/absence of a road within 1km of the site	—	0–1	0.697
Brook trout pres. (binary)	brk1	Invasive species	Presence of brook trout in one or more sample at the site.	—	0–1	0.302
Brook trout pres., v.2 (binary)	brk2	Invasive species	Presence of brook trout in a majority of samples at the site.	—	0–1	0.274
Brook trout pres. in subwatershed (binary)	brkw	Invasive species	Presence of brook trout in one or more samples in the subwatershed	—	0–1	0.44

Note: Prob., probability; Freq., frequency; Elev., elevation; dist, distance. 1 ft = 0.30 m.

represented this with a negative interaction between brook trout presence at the subwatershed scale and UVB distance/presence, such that within subwatersheds with brook trout, the other species would be less likely to occur in UVBs than they would be in subwatersheds without brook trout.

Analyses

We conducted our analyses in several stages. In the first stage we screened each of the hypotheses individually using multilevel logistic regression (a form of generalized linear modeling or GLM), comparing each predictor variable with an intercept-only model using Akaike's information criterion (AIC; Burnham and Anderson 2002). We employed a multilevel modeling approach because our fish collection sites were nonrandom and often strongly clustered (Fig. 1), and likely to violate the parametric assumption of spatial independence of errors. Failing to account for spatial autocorrelation can lead to biases in both the means and standard errors of parameter estimates (Snijders and Bosker 1999; Raudenbush and Bryk 2002; Isaak et al. 2010). Multilevel or hierarchical modeling addresses this problem by modeling errors at more than one level of organization: in addition to the data-level error term, an error term (i.e., a random effect) is included for groups, clusters, or (in our case) subwatersheds (Snijders and Bosker 1999; Raudenbush and Bryk 2002; Gelman and Hill 2007). Multilevel modeling is widely used in the social sciences but has seen fewer applications in ecology (McMahon and Diez 2007), even though it is well suited to modeling naturally hierarchical systems such as streams within subwatersheds (Wagner et al. 2006). We specified a multilevel model with clusters at the subwatershed level, which meant that sites within a subwatershed were assumed to be similar to one another. We verified that the multilevel approach was justified by testing the significance of the random effects using a bootstrapping approach (5000 replicates) implemented in the glmmML package (Broström 2009) in R (R Development Core Team 2009). The test was also repeated with the final fitted models.

We tested for relationships between species occurrence and each of the individual predictors (Table 2), except that brook trout metrics were not tested in brook trout models. We also tested a quadratic form of each of the continuous predictor variables; for example, slope was tested by itself and as slope + slope^2. Quadratic forms were necessary to capture the unimodal relationships hypothesized for some variables, but they were also included for their ability to capture threshold responses better than simple linear predictors. Each model was fit using the glmer function in the lme4 package (Bates and Maechler 2009) using R 2.11 software (R Development Core Team 2009). Predictor variables were standar-

Table 3. Pearson correlations among continuous predictor variables used in analyses of cutthroat trout, bull trout, and brook trout distribution in the Interior Columbia River Basin.

	w2	w1.5	w99	w95	mflow	sflow	vbdist	ptemp	dtemp
w1.5	0.84								
w99	0.75	0.81							
w95	0.72	0.75	0.93						
mflow	–0.09	–0.07	–0.10	–0.14					
sflow	–0.08	–0.06	–0.09	–0.12	0.96				
vbdist	0.04	0.05	0.07	0.09	–0.03	–0.04			
ptemp	0.47	0.42	0.40	0.42	0.09	0.10	0.13		
dtemp	0.56	0.49	0.49	0.52	–0.11	–0.11	0.09	0.91	
slope	0.13	0.10	0.17	0.19	–0.28	–0.30	0.15	0.02	0.14

dized by subtracting the mean and dividing by 2× the standard deviation, which improves both model convergence and interpretation of coefficients (Gelman and Hill 2007). Models were ranked by AIC score.

For several groups of predictors we had correlated candidate metrics (Table 3). There were four metrics of winter high flows, two metrics of baseflow, two metrics of temperature, two metrics related to UVB, and two metrics of brook trout occurrence at the site scale. Correlations among predictors in different groups were generally low, with the exception of correlations between air temperature and winter high flow metrics (r = 0.40–0.56; Table 3). For the screening stage, we wanted to identify the best-supported metric in each group in either its simple or quadratic form, based on AIC score. If no metric in a group had an AIC score better than the intercept-only model we considered the corresponding hypothesis to be unsupported. Once variables were tested individually, we used the best-supported metrics to construct the hypothesized interactions, which we also tested. For example, for a species with vbdist as the best UVB predictor and w95 as the best winter high flow predictor, we evaluated the model vbdist + w95 + vbdist × w95 to test the hypothesized interaction of winter high flows and valley bottom proximity. To be supported, the interaction model needed an AIC score that was better (lower) than the model without the interaction included.

In the second stage of the analysis, we constructed a global model for each species. The global model included the best-supported metric in each group (for hypotheses that were supported), plus all supported interactions. We allowed models to include both a predictor of brook trout at the site and at the subwatershed level because exploratory analyses showed that parameter estimates of the two variables changed little whether they were included separately or together, suggesting that confounding effects of correlation were small. We fit the global model and all possible subsets using the multilevel logistic regression approach described above. We ranked the resulting models by AIC score and retained all models within 6 points of the best overall model as a confidence set of models (Burnham and Anderson 2002), excluding models that were the same as a better-ranked model except for the addition of an uninformative parameter (i.e., one that improved the likelihood by <2; Burnham and Anderson 2002; Arnold 2010). To evaluate the importance of climate in determining the distributions of each species, we compared the best-overall models with reduced models that excluded climate variables. We evaluated the relative importance of geomorphic variables and brook trout the same way. We calculated Akaike model weights (Burnham and Anderson 2002) for the best-overall and the best reduced models (i.e., the no climate, no geomorphic, and no brook trout models). This was a post-hoc analysis that compared only those best models for the sake of illustrating the gain of adding or subtracting climate variables vs. other variables. In addition, for the best overall model we plotted species response curves for each predictor variable by holding all other variables to their mean values and varying the predictor of interest across its full range of values in the dataset.

We conducted a second ranking of all models according to their predictive performance in a form of fourfold cross validation. This involved first dividing the dataset into four geographic regions (Fig. 1). We withheld data from each of the regions in turn, fit the models using data from the other three regions, and predicted presence and absence at sites in the withheld regions (for bull trout, which only occurs in regions 1 and 4, we conducted twofold cross-validation). This form of cross validation provides an indication of model transferability i.e., how well the model would perform in a new region (Fielding and Haworth 1995; Randin et al. 2006). We assessed model performance by constructing 2 × 2 confusion matrices showing correctly and incorrectly predicted presences and absences. In constructing a confusion matrix it is necessary to specify a threshold or cutoff for predicted presence (i.e., the level of predicted probability of occurrence at which a species is assumed to be present) and there are various methods for making this choice (Freeman and Moisen 2008). We determined the optimal cutoff separately for each model as the value between 0.01 and 0.99 (in 0.01 increments) that maximized the true skill statistic (TSS; Allouche et al. 2006), which is defined as sensitivity + specificity – 1. Sensitivity is the proportion of observed presences correctly predicted, and specificity is the proportion of observed absences correctly predicted. The maximum TSS is closely related to the commonly used performance metric AUC, which is the area under the curve of the receiver–operator characteristic plot, and like AUC it has the advantage of being unbiased by prevalence (Manel et al. 2001; Allouche et al. 2006). We used cross-validation maximum TSS (hereinafter, CVTSS) as our measure of cross-validated model performance. We retained a set of best models that included all those with scores within 0.03 points of the best overall. TSS scores potentially range from 0–1 (unless the model is worse than random, in which case it is negative), and this was an arbitrary threshold that retained 3–8 models per species. We evaluated the rela-

Table 4. Support for hypotheses in the first stage of the data analysis, with best-supported metrics for each variable.

		Hypothesis supported? (metric)		
Category	Variable	Brook trout	Bull trout	Cutthroat trout
Climate	Air temperature	**Y** (– dtemp – dtemp^2)	**Y** (– dtemp)	**Y** (– dtemp)
	Winter high flow	**Y** (– w95 + w95^2)	**Y** (– w95)	**Y** (none)
Geomorphic	Stream slope	**Y** (– slope)	**Y** (– slope)	**Y** (– slope – slope^2)
	Unconfined valley bottom	**Y** (– vbdist + vbdist^2)	**N** (+ vbdist)	**Y/N** (+ vbdist – vbdist^2)
	Stream size	**Y** (mflow – mflow^2)	**Y** (+ sflow – sflow^2)	**N** (+ mflow)
Land use	Road presence	**Y** (+ road)	**N** (none)	**N** (none)
Invasive species	Brook trout in site	NA	**N** (none)	**Y** (– brk2)
	Brook trout in subwatershed	NA	**N** (none)[*]	**Y** (– brkw)
Interactions	Winter high flow x valley bottom	**N** (– w95 × vbdist)	**N** (– w95 × vbdist)	**Y** (none)
	Brook trout in subwatershed x valley bottom	NA	**N** (– brkw × vbdist)	**Y** (+ brkw × vbdist)

Note: "Y" means the hypothesis was supported; "N" means it was not. Best-supported metrics are indicated in parentheses; "none" means that no metric was better than an intercept-only model. If a metric is listed for an unsupported hypothesis, it means that the direction of the effect was opposite what was predicted. "NA" means the variable does not apply for that species. "Y (none)" means that no response was predicted and none was observed.

[*] The metric brkw was not supported as a simple predictor for bull trout, but was included in models because the interaction brkw×vbdist was supported.

tive importance of climate variables, geomorphic variables, and brook trout variables by removing all variables in each class, one class at a time, and comparing the CVTSS score of the resulting model to that of the best overall model. We also plotted response curves for the predictor variables in the best overall model.

Results

Tests of individual metrics in the first stage showed support for all climate hypotheses, whereas the invasive species hypotheses were better supported for cutthroat trout than bull trout (Table 4; full results are in Appendix A, Tables A1–A3). Support for geomorphic, land use, and interaction hypotheses were mixed. Notably, hypotheses regarding UVBs, road presence, and interactions were not supported for bull trout, and hypotheses regarding stream size and road presence were not supported for cutthroat trout (Table 4). The random effect for subwatershed was supported for all species for all models ($p \approx 0$).

Brook trout

Brook trout showed a unimodal relationship with dtemp in all of the best-supported models (Tables 5 and 6; Fig. 2*a*). Winter high flow (w95) was also supported in all of the top models based on AIC score and nearly all of the top models based on CVTSS. The relationship was predominantly negative in both cases (Fig. 2*d*). The best nonclimate model had an AIC score nearly 34 points worse, while the best nongeomorphic model had an AIC score over 77 points worse (Tables 5 and 7), indicating that both climate and geomorphic variables were important in describing brook trout distributions. Negative responses to slope, vbdist, and mflow were included in most models in the AIC confidence set, and the top model based on CVTSS (Table 5; Figs. 2*f*, 2*i*, and 2*l*). However, based on CVTSS, the best nongeomorphic model provided nearly as good a fit as the best-overall model CVTSS (Table 5), indicating that climate alone provided good predictions of brook trout occurrence. Although road and the w95 × vbdist interaction were supported in the first stage of analysis and included in the global model, these variables dropped out of all of the top-supported models. Model selection by CVTSS consistently yielded models that were simpler than those selected by AIC, particularly in having fewer second-order terms (Table 5). The highest CVTSS score was 0.366, indicating a 68% overall correct classification rate (classification rate = 0.5(CVTSS + 1)).

Bull trout

Bull trout displayed a strong negative relationship with dtemp in the best-supported models (Tables 6 and 8; Fig. 2*b*). All of the models in the AIC confidence set also included a negative response to w95, but the top model based on CVTSS did not (Tables 6 and 8; Fig. 2*e*). The bull trout response to w95 in the best model by AIC was complicated by the inclusion of an interaction between w95 and vbdist that had a sign opposite the expected direction; that is, bull trout showed a stronger negative response to winter high flows in or near valley bottoms than away from valley bottoms (Fig. 2*e*). However, the uncertainty on the parameter estimate for the interaction term was large (Table 6). The best nonclimate models by both AIC and CVTSS scored much worse than the best-overall models (Tables 7 and 8), indicating that climate variables were critical in describing bull trout distributions. The best nongeomorphic model also had low support, partly because a negative response to slope appeared in all of the models in the AIC confidence set and the top three models based on CVTSS. A positive response to vbdist appeared in some of the models in the AIC confidence set but none of the top models based on CVTSS; conversely, a

Table 5. Brook trout: global model and best-supported models ranked by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	AIC weight	CVTSS
Global model			
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist – vbdist^2 + mflow – mflow^2 + road – w95×vbdist	0.70		
Best models by AIC (AIC confidence set)			
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist – vbdist^2 + mflow – mflow^2	0	25.8%	
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist – vbdist^2 – mflow	0.02	25.6%	
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist + mflow – mflow^2	0.33	21.9%	
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist – mflow	0.34	21.8%	
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist – vbdist^2	4.45	2.8%	
+ dtemp – dtemp^2 – w95 + w95^2 – slope – vbdist	5.01	2.1%	
Best model by AIC, no climate variables			
– slope – vbdist – vbdist^2 + mflow – mflow^2	33.98		
Best model by AIC, no geomorphic variables			
+ dtemp – dtemp^2 – w95 + w95^2 + road	77.15		
Best models by CVTSS			
+ dtemp – dtemp^2 – w95 – slope – vbdist – mflow			0.366
+ dtemp – dtemp^2 – w95 + w95^2			0.364
+ dtemp – dtemp^2 – w95 – slope – vbdist			0.356
+ dtemp – dtemp^2 – w95 – vbdist – slope + mflow – mflow^2			0.352
+ dtemp – dtemp^2 – slope – mflow			0.350
Best model by CVTSS, no climate variables			
– slope – mflow			0.293
Best model by CVTSS, no geomorphic variables			
+ dtemp – dtemp^2 – w95 + w95^2			0.364

Note: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

positive or unimodal response to sflow was included in some of the best models by CVTSS but none of the models in the AIC confidence set. The best model by AIC included a negative response to brkw, though the best nonbrook trout model was also in the confidence set and none of the top models based on CVTSS included brook trout as a predictor variable. The highest CVTSS score was 0.488, indicating a 74% overall correct classification rate.

Cutthroat trout

Cutthroat trout had a weak negative relationship with dtemp in some of the best-supported models (Tables 6 and 9; Fig. 2*c*), and no relationship with winter high flow variables (consistent with our hypothesis). A model without climate variables had strong support by AIC (Tables 7 and 9), and was the best model overall based on CVTSS (Table 9). A negative response to slope and a positive response to mflow appeared in many of the highly ranked models (Table 9; Figs. 2*h* and 2*m*). A response to vbdist was in most of the models, and the best models overall also included the brkw × vbdist interaction. This meant that the cutthroat trout relationship with vbdist depended on whether brook trout were present in the subwatershed: when brook trout were present, cutthroat trout showed a generally negative response, but when brook trout were absent, cutthroat trout showed a neutral to positive response, consistent with our hypothesis (Fig. 2*k*). Cutthroat trout showed a strong response to brook trout presence either at the site or the subwatershed scale (Tables 6 and 9; Fig. 2*o*). This was reflected in the low AIC and CVTSS scores of the best non-brook-trout models (Tables 7 and 9), which were much worse than those of the best-overall models. The highest CVTSS score was 0.426, indicating a 71% overall correct classification rate.

Discussion

Our results suggest considerable variation in the relative importance of factors regulating trout distributions in the ICRB, which has important implications for the species considered. Bull trout distributions were primarily related to climatic variables, with geomorphic variables playing a lesser but still substantial role. Brook trout distributions were influenced strongly by both climatic and geomorphic variables; removing either of these classes of predictors resulted in much weaker models. In contrast, cutthroat trout distributions were weakly associated with climate variables across the range of conditions evaluated in the ICRB, suggesting less sensitivity to climatic trends. Cutthroat trout did, however, display a strong negative response to the presence of nonnative brook trout, which were affected by climatic variables, thereby opening the possibility of an indirect positive response to climate change if brook trout distributions were significantly altered in the future.

Our finding that bull trout was the most temperature-sensitive species is consistent with past work showing that bull trout have lower thermal optima and tolerances than most other salmonids (Selong et al. 2001) and that temperature is an important determinant of the species' distribution (Dunham et al. 2003; Rieman et al. 2007; Isaak et al. 2010). We found

Table 6. Parameter estimates for best-supported models based on Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS) for brook trout, bull trout and cutthroat trout distributions in the interior Columbia River Basin.

	Temperature		Winter high flow		Slope	UVB	
Model	dtemp	$dtemp^2$	w95	$w95^2$	slope	vbdist	$vbdist^2$
Brook trout (AIC)	+0.27±0.28	−1.33±0.33	−1.35±0.31	+0.80±0.20	−0.47±0.15	−1.51±0.24	−0.31±0.20
Brook trout (CVTSS)	+0.08±0.28	−1.31±0.33	−0.50±0.21		−0.54±0.14	−1.31±0.19	
Bull trout (AIC)	−2.38±0.44		−1.52±0.29		−0.80±0.25	+0.55±0.21	
Bull trout (CVTSS)	−3.25±0.44				−0.79±0.25		
Cutthroat trout (AIC)	−0.28±0.23				−0.46±0.13	+0.56±0.36	−0.52±0.19
Cutthroat trout (CVTSS)						−0.15±0.29	

	Size (meanflow)		Brook trout		Interactions	
Model	mflow	$mflow^2$	brk2	brkw	w95×vbdist	vbdist×brkw
Brook trout (AIC)	+0.07±0.35	−0.14±0.11				
Brook trout (CVTSS)	−0.33±0.15					
Bull trout (AIC)				−1.13±0.39	+0.63±0.37	
Bull trout (CVTSS)						
Cutthroat trout (AIC)	+0.62±0.25		−0.85±0.14	−1.21±0.32		+0.72±0.37
Cutthroat trout (CVTSS)				−1.63±0.31		+1.17±0.37

Note: Values are Mean ± SE. Predictor variables have been standardized by subtracting the mean and dividing by 2×SD, so the relative magnitudes of the parameter estimates indicate the importance of the variables.

no lower thermal limit for bull trout; the coldest sites in our dataset were the most likely to be occupied. Brook trout in the ICRB had a unimodal thermal response with a peak in predicted presence at 16 °C air temperature. Unlike the other two species, cutthroat trout in our dataset showed only a slight negative response to temperature. However, this should not be taken as evidence that cutthroat trout are not sensitive to temperature, which has been clearly demonstrated (Bear et al. 2007; Dunham et al. 1999). The muted response may have been because the dataset was confined to the historical range of cutthroat trout, and therefore included few sites that were too warm. Further, detailed post-hoc examination of our results revealed that the relationship between cutthroat trout presence and temperature was complex and did include thresholds at low and high temperatures (~13 °C and ~21 °C). Nevertheless, relative to the other two species cutthroat trout appeared to be less sensitive to thermal variability, at least within the ICRB. Finally, it is important to acknowledge that part of the uncertainty in relationships with temperature is related to using air temperature as a surrogate for water temperatures. Future work to model and predict water temperature is needed to improve predictions of thermal impacts (Isaak et al. 2010).

Our modeling results were generally consistent with the hypothesis that high flows in the post-spawning period restrict fall-spawning trout distributions. We found support for this hypothesis with both model selection methods we employed, although our cross-validation suggested that observed distributions of bull trout could also be explained very well by temperature alone. Two mechanisms have been proposed for this high-flow response. The first is that large floods may cause bed scour sufficient to destroy salmonid redds, embryos, and alevins prior to emergence (Seegrist and Gard 1972; Montgomery et al. 1996; Tonina et al. 2008). The second is that trout are vulnerable to displacement during the first month after emergence from the substrate (Nehring and Anderson 1993; Fausch et al. 2001) because they cannot yet hold position in high-velocity water (Heggenes and Traaen 1988; Crisp and Hurley 1991). The first mechanism involves large events (as measured by our metrics w1.5 or w2) while the second can be caused by smaller events (such as correspond to the w95 and w99 metrics). We found that for brook and bull trout, the best-supported predictor was w95, which is consistent with the second mechanism. This is not strong evidence, however, and additional research would be needed to disentangle these two hypotheses.

All three species were less likely to occur as stream slope increased. This contrasts with previous studies (Fausch 1989; Hilderbrand 1998; Dunham et al. 1999) that found that cutthroat trout occurred more frequently in higher gradient reaches, whereas brook trout occurred in lower gradient reaches. However, previous studies (Fausch 1989) also noted that such a pattern could have resulted from brook trout excluding cutthroat trout rather than a habitat preference per se. Our analysis was less confounded because our broad coverage allowed us to model cutthroat trout response to slope in both sympatry and allopatry with brook trout, better separating the slope effect from the brook trout effect. Another geomorphic variable, stream size, was supported as a predictor variable for all species in the screening stage, but dropped out of later models for bull trout and some models for cut-

Fig. 2. Species response to continuous predictor variables for the best overall models by Akaike information criterion (AIC, grey line) and cross validated predictive performance (CVTSS, black line). For parameters with interactions (panels e, j and k), broken lines indicate responses at alternative levels of the interacting variable, as noted.

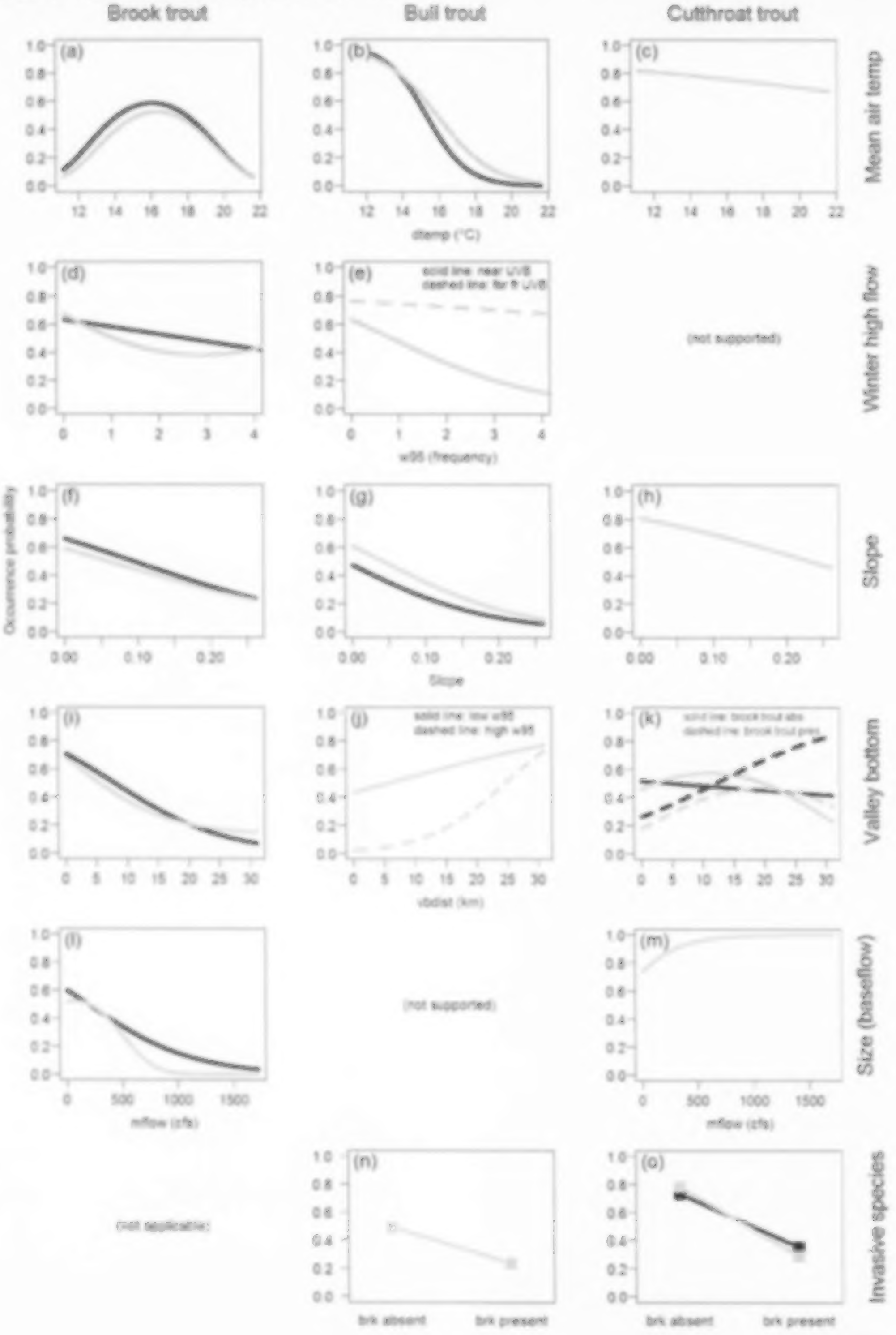


Table 7. Best models for brook trout, bull trout, and cutthroat trout with and without variables for climate, geomorphic, and invasive species, ranked by Akaike's information criterion (AIC).

Model	Delta AIC	Model weight
Brook trout		
Best overall	0	100%
Best no climate	34.0	0%
Best no geomorphic	77.2	0%
Bull trout		
Best overall	0	95%
Best no climate	91.2	0%
Best no geomorphic	16.5	0%
Best no invasives	6	5%
Best overall		
Best overall	0	61%
Best no climate	0.9	39%
Best no geomorphic	33.0	0%
Best no invasives	58.4	0%

Note: Model weights are calculated as if the models listed (the best-supported in each category) were the only candidate models.

throat trout, indicating that apparent associations with stream size were better explained by other variables. All brook trout models showed that occurrence probability declined as stream size increased, consistent with hypotheses and previous observations (Rahel and Nibbelink 1999; Dunham et al. 2002; Öhlund et al. 2008).

Brook trout had a positive association with UVBs, which is consistent with past observations (Collen and Gibson 2001; Dunham et al. 2002; Benjamin et al. 2007). However, contrary to our hypotheses and past research (Baxter and Hauer 2000), we found a negative association of bull trout with UVBs. We had hypothesized that this negative relationship was an indirect response to brook trout occupying UVBs and excluding bull trout, and tested for this by modeling an interaction between brook trout presence and UVB distance. This interaction was not supported by AIC or CVTSS. At present we have no alternative hypotheses to explain the observed bull trout – UVB relationship. In contrast, cutthroat trout displayed a negative relationship with UVBs only in subwatersheds with brook trout present, supporting the hypothesis that brook trout excluded cutthroat trout from these otherwise favorable habitats. The reason that brook trout use and appear to dominate UVBs is not completely clear. It has long been known that brook trout favor sites with groundwater upwelling for spawning (Benson 1953; Witzel and MacCrimmon 1983), probably because the warmer groundwater provides favorable conditions for egg incubation (Curry et al. 1995). Therefore, the high degree of hyporheic exchange typical of channels in UVBs (Baxter and Hauer 2000) may explain the higher probability of occurrence of brook trout. In addition, the lack of confinement of UVBs results in high sinuosity and abundant low-gradient, off-channel water storage, particularly when beavers are present (Johnston and Naiman 1987). We hypothesized that these areas would provide a velocity refuge for redds and juvenile trout during periods of high flow (Shellberg et al. 2010). We tested for this by modeling an interaction between valley bottoms and high flows; results showed that for both brook trout and bull trout the interaction was supported but the sign was opposite the expected direction. This result is confusing, but at a minimum indicates that there is no support for the velocity-refuge hypothesis in this dataset.

We found strong support for the hypothesis that cutthroat trout were less likely to occur when brook trout were present at the site or within the subwatershed (Gresswell 1988; Dunham et al. 2002; Peterson et al. 2004*a*). We found weaker evidence for a negative response of bull trout to brook trout presence at the subwatershed scale. Previous studies also reported mixed results on brook trout/bull trout co-occurrence and suggested spatial variability in the nature of the interactions (Dunham and Rieman 1999; Rich et al. 2003; Rieman et al. 2006). An exploration of spatial variability in biotic interactions was beyond the scope of our study, but this would be a promising avenue for future analyses using this dataset.

Roads were predictive of the presence of nonnative brook trout in the first stage of our data analysis, but did not explain presence of native trout. This stands in contrast to past work on native trout in the region (Rieman et al. 1997; Thurow et al. 1997), and the diverse range of negative impacts that roads can have on aquatic ecosystems and species (Trombulak and Frissell 2000). The lack of land use effects may reflect that most study sites were in relatively pristine areas, since the sampling design of many of the original datasets was intended to detect native cutthroat and bull trout. Alternatively, our predictor variable may simply have been too crude an indicator of human land use alteration. Accordingly, results of this work should not be construed to suggest that roads do not pose threats to native trout.

Modeling issues and limitations

We used multiple techniques to attempt to identify which predictor variables had support across the geographic range of the dataset and therefore represented general, consistent relationships. We found that models selected by CVTSS had fewer predictors and second-order terms than those selected by AIC. This suggests that in terms of model transferability (Fielding and Haworth 1995; Randin et al. 2006), selection by AIC resulted in models that were somewhat overfit; the simpler models are probably more appropriate for predictions in new locations and under new climatic conditions. Nevertheless, there is value in examining the models selected by AIC, because these describe species responses to predictors across the full dataset and the entire region and therefore incorporate all available information. Variables supported by AIC but not CVTSS merit further study and perhaps regional-scale analysis. Many variables were supported by both methods, though, providing strong evidence in favor of the associated hypotheses.

Cross validation indicated that the best GLM models had classification success rates of 66%–74%. This suggests that even with the best models there is a significant amount of unexplained variability in species distributions. We suspect a major reason is the lack of information on local factors that play a role in determining species presence, including movement barriers (Fausch et al. 2009) and stocking histories (Paul and Post 2001). Other potential influences could include uncertainty contributed by lumping together data represented by different life stages (e.g., juveniles versus adults)

Table 8. Bull trout: global model and best-supported models by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	Model weight	CVTSS
Global model			
– dtemp – w95 – slope + vbdist + sflow – sflow^2 – brkw + w95×vbdist – brkw×vbdist	7.59		
Best models by AIC (AIC confidence set)			
– dtemp – w95 – slope + vbdist – brkw + w95×vbdist	0	43.7%	
– dtemp – w95 – slope + vbdist – brkw	0.87	28.3%	
– dtemp – w95 – slope + vbdist + sflow – brkw + w95×vbdist	1.23	23.7%	
– dtemp – w95 – slope – brkw	6.02	2.2%	
– dtemp – w95 – slope + vbdist + w95×vbdist	6.05	2.1%	
Best model by AIC, no climate variables			
vbdist – slope – brkw – brkw×vbdist	91.22		
Best model by AIC, no geomorphic variables			
– dtemp – w95	16.49		
Best model by AIC, no brook trout variables			
– dtemp – w95 – slope + vbdist – w95×vbdist	6.05		
Best models by CVTSS			
– dtemp – slope			0.488
– dtemp – w95 – slope			0.479
– dtemp – slope + sflow – sflow^2			0.477
– dtemp + sflow – sflow^2			0.476
– dtemp – w95 + vbdist – slope + sflow – sflow^2			0.473
– dtemp + sflow			0.472
– dtemp			0.472
– dtemp – slope + sflow			0.470
Best model by CVTSS, no climate variables			
+ vbdist + sflow			0.344
Best model by CVTSS, no geomorphic variables			
– dtemp			0.472
Best model by CVTSS, no brook trout variables			
– dtemp – slope			0.488

Note: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

and the timing of sample collection within the summer – early fall low-flow season. For cutthroat trout and bull trout, there was a great deal of model uncertainty in the results based on cross validation; models with very different sets of variables had almost equal support. For cutthroat trout it was clear that the presence of brook trout was critically important, but the role of other variables was less certain. Similarly, for bull trout, only temperature was an essential predictor variable; a number of other variables had varying levels of support. These issues do not alter the main conclusions of this study (a strong role of climate in determining brook trout and bull trout distributions, and a strong effect of brook trout on cutthroat distributions), but we would caution against making predictions based on any single model or at fine spatial scales (e.g., individual stream reaches or subwatersheds).

A final concern is that our methods did not explicitly address imperfect detection. Although methods exist to incorporate imperfect detection in occupancy modeling (MacKenzie et al. 2002), doing so in a multilevel modeling framework is complex (Wenger et al. 2008), and we judged it to be of limited benefit. Our dataset consisted of samples collected using multipass electrofishing (one or more surveys) and snorkeling (four or more surveys). Past studies have shown that multipass electrofishing capture efficiency (i.e., chance of detecting a single individual) of the species considered here is approximately 40%–60% (Peterson et al. 2004*b*). Even assuming the low end of this range, this implies that if there were 5 individual fish at a site, the chances of detecting at least one was >92%; if there were 10 fish, the chance of detecting one or more was >99%. Therefore, in our dataset only sites with very low abundances of fish were likely to be incorrectly labeled as absences, which we contend is reasonable, since sites with very few individuals are not likely to represent optimal habitat or persistent populations for that species. In any case, assuming that there is no large bias to patterns of capture efficiency, the principal consequence of ignoring incomplete detection is to underestimate the magnitude of covariates (Tyre et al. 2003), which implies that our hypothesis tests are somewhat conservative.

Conservation and management implications

Our results indicate a high climate sensitivity for brook trout and bull trout, consistent with previous studies (Flebbe et al. 2006; Rieman et al. 2007; Isaak et al. 2010), but poten-

Table 9. Cutthroat trout: global model and best-supported models by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	Model weight	CVTSS
Global model			
– dtemp – brk2 – brkw + vbdist – vbdist^2 + brkw×vbdist + mflow – slope – slope^2	1.89		
Best models by AIC (AIC confidence set)			
– dtemp – brk2 – brkw + vbdist – vbdist^2 + brkw×vbdist + mflow – slope	0	28.2%	
– dtemp – brk2 – brkw + vbdist – vbdist^2 + mflow – slope + slope^2	0.27	24.7%	
– brk2 – brkw + vbdist – vbdist^2 + brkw×vbdist + mflow – slope	0.93	17.7%	
– brk2 – brkw + vbdist – vbdist^2 + mflow – slope – slope^2	1.99	10.4%	
– dtemp – brk2 – brkw – vbdist + brkw×vbdist + mflow – slope + slope^2	2.60	7.7%	
– brk2 – brkw + vbdist – vbdist^2 + mflow – slope	3.38	5.2%	
– brk2 – brkw – vbdist + brkw×vbdist + mflow – slope + slope^2	4.07	3.7%	
– dtemp – brk2 – brkw – vbdist + brkw×vbdist + mflow – slope	4.98	2.3%	
Best model by AIC, no climate variables			
– brk2 – brkw + vbdist – vbdist^2 + brkw×vbdist + mflow – slope	0.93		
Best model by AIC, no geomorphic variables			
– dtemp – brk2 – brkw	32.97		
Best model by AIC, no brook trout variables			
+ vbdist – vbdist^2 + mflow – slope + slope^2	58.40		
Best models by CVTSS			
– brkw – vbdist + brkw×vbdist			0.426
– dtemp – brk2 + vbdist – vbdist^2 – slope + mflow			0.426
– dtemp – brkw – vbdist + brkw×vbdist			0.423
– brk2			0.422
– brkw – slope + vbdist + mflow			0.421
– brkw + vbdist			0.416
– brkw – slope + mflow			0.415
– brkw – dtemp – slope + mflow			0.414
– brkw + mflow			0.413
Best model by CVTSS, no climate variables			
–brkw – vbdist + brkw×vbdist			0.426
Best model by CVTSS, no geomorphic variables			
– brk2			0.422
Best model by CVTSS, no brook trout variables			
– dtemp + mflow – slope – slope^2			0.388

Notes: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

tially low climate sensitivity for cutthroat trout, in contrast to earlier work (Dunham et al. 1999; Bear et al. 2007; Williams et al. 2009). Our results also suggest that the presence of brook trout is the single largest influence on cutthroat trout distribution in the ICRB, implying that future climate changes may alter cutthroat trout distributions indirectly via changes to brook trout distributions. If brook trout respond more negatively to warming temperatures than do cutthroat trout, as suggested by our results, then the net outcome of a warming climate could be favorable to cutthroat trout. An increase in frequency of winter high flow events (as would be expected with warming; Elsner et al. 2010) could further stress brook trout populations. Ours is not the first study to suggest that climate change could provide some benefit to cutthroat trout. Cooney et al. (2005) speculated that because cutthroat trout in the central and southern Rocky Mountains are often confined to headwater refugia in which cold temperatures limit productivity and recruitment (Isaak and Hubert 2004; Young and Guenther-Gloss 2004; Coleman and Fausch 2007), warming could increase population sizes (assuming that base flows remain adequate to support upstream expansion). Such an outcome is far from certain, however. Isaak et al. (2010) recently projected that warming of some Rocky Mountain streams could cause an upward shift in elevation of rainbow trout populations with little net change in habitat area. The same could occur with brook trout. There may be additional small, high-elevation streams that could become more suitable for brook trout in the future, enabling an upward shift in elevation with no net loss in habitat. Further research is needed to determine the likely trajectories of brook trout and cutthroat trout under different climatic and landscape conditions. Our scenario for cutthroat trout also ignores the potential range expansion of other native or introduced species with even higher temperature tolerances, such as brown trout and smallmouth bass (*Micropterus dolomieu*), which could prove to have strong negative interactions with cutthroat trout.

Bull trout is the most climate sensitive of the trout species considered here. Its strong temperature sensitivity, coupled with a likely sensitivity to an increase in winter high flow frequency, mean that a warming climate in the ICRB will likely lead to losses of suitable habitat. Our analysis indicates that the species already inhabits the coldest available streams, so unlike brook trout, it does not have the potential to shift to higher elevation habitats.

Our results have several implications for management. The first is that in locations that (*i*) support both cutthroat trout and brook trout but (*ii*) are warmer than optimal for brook trout and (*iii*) have high flows in the winter, brook trout control efforts may be highly feasible and provide significant benefits to cutthroat trout. Second, preventing brook trout from accessing uninvaded UVBs may be important for protecting habitat for native trout, as removal of established populations of brook trout from UVBs is unlikely to be effective (e.g., Meyer et al. 2006). Third, areas where brook trout currently dominate over cutthroat trout still have conservation value, because these locations may become less hospitable to brook trout and more so to cutthroat trout in the future. An important intermediate management step in these locations may be to guard against the invasion of warm-water species, perhaps using barriers to upstream migration (Fausch et al. 2009) and through the application of distributional monitoring protocols (Isaak et al. 2009) that facilitate the early detection of invasions and increase the chances of population eradication. Finally, our results reinforce those of other researchers (e.g., Rieman et al. 2007; Isaak et al. 2010) that suggest effective long-term management for bull trout in the face of climate change will require prioritization to ensure that resources are allocated to those locations with the coldest temperatures that offer the greatest long-term potential to sustain the species.

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Appendix A

Appendix A appears on the following pages.

Table A1. Brook trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
w95 + vbdist + w95×vbdist	**3435**	**−0.65±0.18**	**−1.32±0.18**	**0.56±0.32**
w95 + vbdist	3436	−0.64±0.18	−1.39±0.18	
vbdist + vbdist^2	**3442**	**−1.79±0.23**	**−0.50±0.19**	
vbdist	3448	−1.26±0.18		
slope	**3480**	**−0.75±0.13**		
slope + slope^2	3482	−0.80±0.17	0.07±0.16	
w95 + w95^2	**3488**	**−1.49±0.28**	**0.77±0.20**	
dtemp + dtemp^2	**3490**	**−0.08±0.26**	**−1.47±0.34**	
ptemp + ptemp^2	3490	0.36±0.25	−1.30±0.28	
mflow + mflow^2	**3498**	**1.00±0.31**	**−0.38±0.11**	
w95	3500	−0.66±0.18		
sflow + sflow^2	3501	0.95±0.32	−0.41±0.12	
vbpres	3501	−0.44±0.12		
road	**3505**	**0.41±0.14**		
w1.5 + w1.5^2	3505	−0.60±0.25	0.39±0.12	
w99	3507	−0.52±0.20		
w99 + w99^2	3508	−0.78±0.31	0.20±0.18	
w2 + w2^2	3508	−0.58±0.23	0.41±0.17	
dtemp	3508	−0.50±0.23		
(intercept only)	3511			
w2	3512	−0.20±0.17		
ptemp	3512	−0.25±0.21		
mflow	3512	−0.14±0.12		
sflow + sflow^2	3512	−0.12±0.12		
w1.5	3513	−0.02±0.17		

Note: Akaike information criterion (AIC) scores and parameter estimates (mean ± SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.

Table A2. Bull trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
w95 + vbdist + w95×vbdist	**984**	**−2.20±0.27**	**0.36±0.19**	**−0.64±0.35**
w95 + vbdist	985	−2.08±0.26	0.37±0.19	
w95	**987**	**−2.14±0.26**		
w99	988	−2.47±0.32		
w95 + w95^2	989	−2.04±0.46	−0.12±0.44	
w99 + w99^2	989	−2.22±0.51	−0.30±0.54	
dtemp	**994**	**−3.48±0.43**		
dtemp + dtemp^2	996	−3.41±0.52	−0.19±0.89	
w2	1017	−1.84±0.28		
w2 + w2^2	1018	−1.65±0.36	−0.33±0.42	
w1.5	1026	−1.75±0.30		
w1.5 + w1.5^2	1027	−2.01±0.38	0.24±0.24	
slope	**1044**	**−1.24±0.25**		
slope + slope^2	1046	−1.23±0.34	−0.02±0.25	
sflow + sflow^2	**1061**	**0.91±0.29**	**−0.11±0.05**	
mflow + mflow^2	1062	0.77±0.27	−0.06±0.03	
mflow	1062	0.45±0.18		
sflow	1062	0.46±0.18		
vbdist	**1063**	**0.54±0.20**		
brkw + vbdist + brkw×vbdist	**1063**	**−0.23±0.45**	**1.02±0.36**	**−0.75±0.43**
brkw + vbdist	1064	−0.41±0.43	0.51±0.20	
vbdist + vbdist^2	**1065**	**0.47±0.36**	**−0.05±0.23**	
ptemp	1065	−0.55±0.27		
ptemp + ptemp^2	1067	−0.84±0.42	0.32±0.36	
(intercept only)	1067			
brkw	1068	−0.60±0.44		
brk1	1069	0.19±0.23		
brk2	1069	−0.02±0.26		
road	1069	−0.01±0.27		
vbpres	1069	0.01±0.28		

Note: Akaike information criterion (AIC) scores and parameter estimates (mean±SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.

Table A3. Cutthroat trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
brk2	**3327**	**−1.08±0.14**		
brkw + vbdist + brkw×vbdist	**3341**	**−1.63±0.31**	**−0.15±0.29**	**1.17±0.37**
brk1	3343	−0.91±0.13		
brkw + vbdist	3350	−1.40±0.30	0.59±0.17	
brkw	3358	−1.75±0.31		
mflow	**3363**	**0.91±0.25**		
mflow + mflow^2	3364	0.66±0.44	0.15±0.29	
sflow	3365	0.80±0.21		
sflow + sflow^2	3367	0.97±0.33	−0.07±0.11	
vbdist + vbdist^2	**3368**	**1.05±0.23**	**−0.48±0.18**	
vbdist	3372	0.68±0.18		
w99 + vbdist	3374	0.00±0.20	0.70±0.18	
w99×vbdist	3374	0.15±0.20	0.69±0.18	−0.40±0.38
slope + slope^2	**3377**	**−0.18±0.17**	**−0.26±0.15**	
slope	3378	−0.38±0.12		
dtemp	**3383**	**−0.48±0.22**		
dtemp + dtemp^2	3384	−0.32±0.26	−0.34±0.28	
vbpres	3384	0.24±0.13		
(intercept only)	3385			
road	3385	−0.21±0.14		
w99 + w99^2	3385	−0.39±0.33	0.44±0.23	
w2	3386	−0.17±0.16		
w99	3387	0.11±0.20		
w1.5	3387	−0.06±0.18		
w95	3387	−0.03±0.18		
ptemp	3387	0.01±0.21		
w95 + w95^2	3388	−0.32±0.29	0.27±0.23	
w2 + w2^2	3388	−0.03±0.24	−0.15±0.20	
ptemp + ptemp^2	3388	−0.13±0.25	0.25±0.25	
w1.5 + w1.5^2	3389	−0.09±0.26	0.03±0.15	

Note: Akaike information criterion (AIC) scores and parameter estimates (mean ± SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.

Effects of landscape variables and season on reference water chemistry of coastal marshes in eastern Georgian Bay

Rachel deCatanzaro and Patricia Chow-Fraser

Abstract: We surveyed 34 marshes in relatively pristine Precambrian Shield catchments in Georgian Bay and related water chemistry to a suite of landscape-level variables, including characteristics of the marsh and its drainage basin. The first landscape principal component (explained 48% of variation) ordered marshes along a gradient with high values corresponding to marshes with large watersheds that contain extensive upstream wetland and that receive relatively high precipitation inputs. This axis was negatively related to specific conductivity, pH, nitrate nitrogen, and SO_4^{2-} concentrations and positively related to total phosphorus, colour, suspended solids, ammonia nitrogen, and summer dissolved organic carbon. Stepwise regression models built using catchment- and marsh-level variables explained up to 64% of the variation in water chemistry variables. Average precipitation and snowmelt inputs to the catchments were first to enter the majority of models, alone explaining up to 43% of the variation (in the case of water colour), while drainage area alone explained 44% of the variation in pH. Concentrations of catchment-derived constituents in marshes were highest in spring, reflecting greater loadings from the watersheds, while ionic strength was highest during summer, reflecting increased contributions form other sources (i.e., lake water).

Résumé : Nous avons inventorié 34 marécages dans des bassins hydrographiques relativement peu modifiés dans la baie Géorgienne sur le Bouclier canadien et avons relié la chimie de l'eau à une série de variables à l'échelle du paysage, en particulier aux caractéristiques des marécages et de leur bassin versant. La première composante principale du paysage (qui explique 48 % de la variation) place les marécages le long d'un gradient dont les valeurs supérieures correspondent à des marécages à bassin versant de grande superficie qui contient en amont d'importantes terres humides et qui reçoit de apports relativement élevés des précipitations. Cet axe est en corrélation négative avec la conductivité spécifique, le pH et les concentrations de SO_4^{2-} et d'azote sous forme de nitrates et en corrélation positive avec le phosphore total, la couleur, les solides en suspension, l'azote sous forme d'ammoniaque et le carbone organique dissous en été. Des modèles de régression pas à pas construits à partir des variables à l'échelle du bassin versant et du marécage expliquent jusqu'à 64 % de la variation des variables de chimie de l'eau. Les apports moyens des précipitations et de la fonte des neiges aux bassins versants sont les premières variables à entrer dans la plupart des modèles, expliquant à elles seules jusqu'à 43 % de la variation (dans le cas de la couleur de l'eau), alors que la surface du bassin versant seule explique 44 % de la variation du pH. Les concentrations des composantes provenant du bassin versant sont le plus élevées au printemps, ce qui indique de plus forts apports à partir du bassin hydrographique, alors que la force ionique est au maximum durant l'été, ce qui reflète les contributions accrues à partir d'autres sources (c'est-à-dire l'eau du lac).

[Traduit par la Rédaction]

Introduction

Great Lakes coastal marshes are highly productive (Jude and Pappas 1992) and dynamic (Keough et al. 1999) ecosystems with hydrologic connections to both their watershed and the adjoining lake. Human activities such as water-level manipulation and land development have had major impacts on coastal marsh dynamics in many parts of the Great Lakes (Mayer et al. 2004). Urban and agricultural development can be particularly detrimental, causing increases in nutrient loadings and turbidity (Crosbie and Chow-Fraser 1999; Morrice et al. 2008) that result in shifts in trophic status and species assemblages (Jude and Pappas 1992; Lougheed et al. 2001; Seilheimer and Chow-Fraser 2006). Wetlands vary in their sensitivity to altered hydrology and watershed dynamics, and it is widely recognized that to ensure proper management of these ecosystems, a better understanding of the natural hydrologic and geologic factors controlling the conditions of coastal wetlands is critical (Keough et al. 1999; Mayer et al. 2004; Morrice et al. 2004).

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Within forested landscapes, catchment morphology can exert a strong influence on the natural chemistry of surface waters. Landscape-level studies on inland lakes of the Boreal Plains of Alberta (Devito et al. 2000; Prepas et al. 2001) and the Precambrian Shield region of southern Quebec (D'Arcy and Carignan 1997) and south-central Ontario (e.g., Dillon

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et al. 1991; Dillon and Molot 1997; Eimers et al. 2008) have provided some insight into the relationships between catchment features and lake chemistry. A number of these studies have found that wetland cover, drainage slope, and catchment or drainage area are among the strongest predictors of nutrient and ion concentrations and lake productivity (e.g., D'Arcy and Carignan 1997; Dillon and Molot 1997; Prepas et al. 2001). Precipitation can play a large role in the export of nutrients and sediments to streams and lakes by generating runoff that interacts with catchment features and promotes flushing of allochthonous materials (Allan et al. 1993; Schiff et al. 1998; Eimers et al. 2008). Great Lakes coastal wetlands are distinct from other freshwater inland systems in that their hydrology and chemistry are further influenced by large-lake processes through a direct hydrological connection (Mayer et al. 2004). Strength of hydrologic connections to watershed and lake, and thus nutrient fluxes, vary seasonally and with site morphology; under scenarios of high watershed discharge relative to seiche-driven flow (e.g., spring snowmelt), lake water inflow and mixing in the wetland is reduced, and the chemistry of the marsh is more heavily influenced by runoff chemistry (Trebitz et al. 2002; Morrice et al. 2004). This is similar to the interaction of river flow and tides in coastal estuaries and salt marshes (see Duxbury 1979).

Coastal marshes of the Precambrian Shield portion of eastern Georgian Bay are among the least human-disturbed in the Great Lakes Basin (Chow-Fraser 2006; Cvetkovic et al. 2010) and afford a unique opportunity to study water chemistry dynamics in the absence of major anthropogenic perturbations. Expansion of road networks and incremental cottage and residential development are expected to continue (see deCatanzaro et al. 2009), and many climate models have predicted changes in precipitation patterns and a drop in Lake Huron water level (see Mortsch and Quinn 1996; Lofgren et al. 2002), making the establishment of reference conditions of critical importance for this area. The majority of the marshes form in lacustrine protected embayments, which are characterized as having strong surface-water connections with the lake (see Albert et al. 2005). Climatic conditions promote snow accumulation during winter, resulting in high hydrologic flow from watersheds during spring snowmelt, and this could have important consequences for the relative influences of watershed versus lake on the hydrology and chemistry of coastal marshes (Morrice et al. 2004).

This is the first paper to examine the relative effects of watershed features and processes (including precipitation inputs) and marsh morphology on reference water chemistry of coastal marshes in eastern Georgian Bay. We predict that marshes with larger drainage areas receiving higher precipitation and snowmelt inputs would have water chemistry that more closely reflects processes in watersheds of the Precambrian Shield with respect to sediment and nutrient retention and export. On the other hand, the chemistry of marshes with weak hydrologic connection to uplands would be more similar to that of open Georgian Bay. We also expect features such as catchment slope to play a major role, whereby water chemistry would reflect higher nutrient and sediment export from steeply sloped catchments. Secondly, we examine seasonal changes in marsh water chemistry by (*i*) comparing discrete survey data from each of the marshes in spring and summer and (*ii*) monitoring continuous changes in water chemistry at a representative marsh from ice-out to early autumn. Consistent with previous studies, we expect the highest concentrations of catchment-derived constituents in marshes during spring, when snowmelt produces high discharge and nutrient loadings to downstream areas. Our results will help to reveal the relative importance of watershed versus Great Lakes influences on water quality of these pristine systems that are known to support high biodiversity of plants, fish, and species at risk (Croft and Chow-Fraser 2009; Cvetkovic et al. 2010; deCatanzaro and Chow-Fraser 2010) and will inform the discussion on how best to adapt to changes in precipitation and runoff patterns in this region associated with climate change.

Materials and methods

Study area

We selected 34 coastal marshes in protected embayments with predominantly forested watersheds and minimal human disturbance (no roads in the watershed and no cottages directly bordering the marsh). The marshes are situated between northern Musquash Channel and Woods Bay on the eastern shore of Georgian Bay (Fig. 1). The landscape is characterized by thin (about 30 cm), sandy, acidic, patchy soils, where Precambrian Shield bedrock is exposed between areas of vegetated till deposits and wetlands (Weiler 1988). Landward vegetation is predominantly a mix of second-growth deciduous and coniferous forests of the Great Lakes – St. Lawrence Forest region, characterized by species such as eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), eastern hemlock (*Tsuga canadensis*), white spruce (*Picea glauca*), sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), and American beech (*Fagus grandifolia*). Extensive wetland complexes form in topographic depressions and along streams and tributaries flooded as a result of beaver (*Castor canadensis*) activity.

Within this area, the offshore Georgian Bay water is alkaline and has high specific conductivity (COND; N. Diep, Ontario Ministry of the Environment, Great Lakes Unit of the Water Monitoring and Reporting Section, 125 Resources Road, Etobicoke, ON M9P 3V6, unpublished data; Table 1) owing to the influence of dissolved ions from easily eroded Palaeozoic limestone that surrounds the south and the west of Georgian Bay (i.e., Bruce Peninsula of the Niagara Escarpment; Weiler 1988). Offshore total phosphorus (TP) concentrations range from around 7.0 $\mu g \cdot L^{-1}$ in spring to 3.9 $\mu g \cdot L^{-1}$ in summer, while sulphate (SO_4^{2-}) is over 10 $mg \cdot L^{-1}$ and nitrate nitrogen (TNN) over 200 $\mu g \cdot L^{-1}$ during the ice-free season. Concentrations of ammonia nitrogen (TAN), dissolved organic carbon (DOC), colour (COL), and total suspended solids (TSS) are all low in the open-water areas. The climate is characterized by extremes of cold and dry or hot and humid weather. Winter temperatures are below freezing for up to 4 months of the year, while summers have a mean July temperature of 18 °C. Average annual precipitation is around 1000 mm. Snowmelt and the majority of high runoff typically occur in March and April (Weiler 1988).

Landscape analyses

Analyses of landscape variables were performed in ArcGIS 9.2 (ESRI, Redlands, California, USA). We delineated marsh

Figure 1. Map of the 34 study sites (*b*) and their location in the Great Lakes basin (*a*). Black Rock marsh watershed is highlighted in panel (*b*) and shown in greater detail in panel (*c*).

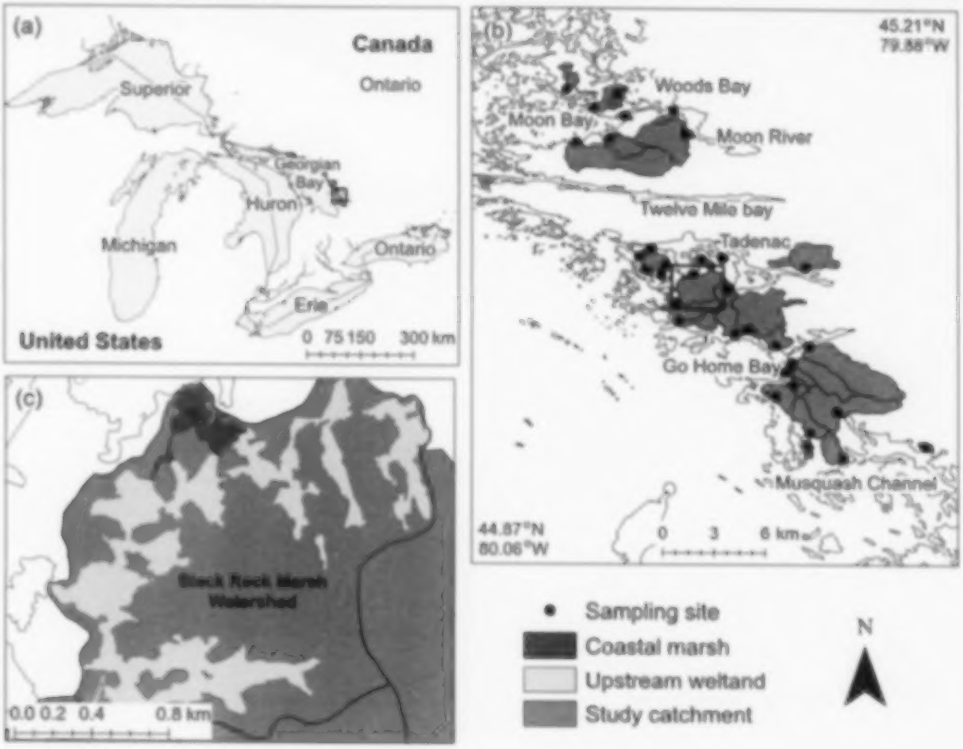

(a)
Canada
Ontario
Superior
Georgian Bay
Huron
Michigan
Ontario
Erie
United States
0 75 150 300 km
(b)
45.21°N
79.88°W
Woods Bay
Moon Bay
Moon River
Twelve Mile bay
Tadenac
Go Home Bay
Musquash Channel
44.87°N
80.06°W
0 3 6 km
(c)
Black Rock Marsh Watershed
0.0 0.2 0.4 0.8 km
Sampling site
Coastal marsh
Upstream weltand
Study catchment
N

Table 1. Means and ranges of water chemistry variables (spring–summer averaged) in offshore open-water sites and in coastal marshes.

		Open water (n = 11)[a]		Coastal marsh (n = 33)	
Parameter	Abbreviation	Mean	Range	Mean	Range
Group 1					
Total phosphorus ($\mu g \cdot L^{-1}$)	TP	5.5	4.0–7.8	16.4	9.3–33.8
Soluble reactive phosphorus ($\mu g \cdot L^{-1}$)	SRP	0.6	0.5–1.0	5.2	2.4–10.9
Total ammonia nitrogen ($\mu g \cdot L^{-1}$)	TAN	8	4–12	15	5–90
Dissolved organic carbon ($mg \cdot L^{-1}$)	DOC	2.5	2.0–3.1	16.6	8.3–69.1
Colour (mg Pt$\cdot L^{-1}$)	COL	5	1–9	116	43–337
Total suspended solids ($mg \cdot L^{-1}$)	TSS	0.8	0.6–1.3	2.8	0.9–11.4
Group 2					
Total nitrate-nitrite nitrogen ($\mu g \cdot L^{-1}$)	TNN	225	190–259	18	8–85
Sulphate ($mg \cdot L^{-1}$)	SO_4^{2-}	11.1	7.5–12.8	1.4	0.5–6.0
Specific conductivity ($\mu S \cdot cm^{-1}$)	COND	180	159–196	36	15–92
pH	—	8.1	8.0–8.2	6.7	6.1–7.5

Note: Back-transformed geometric means are reported for variables that were $\log_{10}$-transformed.

[a] Offshore data were obtained from the Ontario Ministry of the Environment in 2005 (N. Diep, Ontario Ministry of the Environment, Great Lakes Unit of the Water Monitoring and Reporting Section, 125 Resources Road, Etobicoke, ON M9P 3V6, unpublished data).

drainage basins by using digitized contours and spot elevations of Ontario base maps (1:10 000; Ontario Ministry of Natural Resources) and applying traditional cartographic procedures. Delineations were made with contours overlain on 2002 1 m resolution IKONOS satellite images to facilitate identification of surface drainage networks. Drainage basin area (DBA) was calculated from watershed polygons (Table 2). We determined average slope (SLOPE) for each watershed

Table 2. Description of landscape variables used in analyses.

Variable	Description
AQUAT	Size of coastal marsh (aquatic portion)
MED	Total area of meadow marsh connected to the aquatic marsh
OPEN	Width of surface water connection to Georgian Bay
DBA	Drainage basin area (excluding aquatic marsh)
WET	Total area of wetland (bog, fen, swamp, marsh, beaver ponds) located upstream of the coastal marsh
SLOPE	Mean drainage basin slope
DBA/AQUAT	Drainage ratio (ratio of drainage basin area to aquatic marsh area)
PROPWET	Proportion of the drainage basin occupied by upstream wetland
PREC$_{07, 14, 30}$	Catchment inputs of precipitation and snowmelt over 7-, 14-, or 30-day periods prior to sampling

by using the Provincial Digital Elevation Model (10 m resolution; Ontario Ministry of Natural Resources) and the Spatial Analyst extension of ArcGIS 9.2.

To identify and quantify wetland areas within each catchment, we used the McMaster Coastal Wetland Inventory (P. Chow-Fraser, unpublished data). This inventory was created from the same 2002 IKONOS imagery used to examine surface-water connections. Wetlands upstream of the marsh (WET) that fell within the watershed (also expressed as a proportion of the total watershed area; PROPWET) consisted of a combination of newly formed beaver ponds, fens, marshes, swamps, and bogs. Meadow marsh (MED) occurred landward of the shoreline boundary and consisted predominantly of sedges and shrubs, with saturated soils near the surface but without standing water for most of the year. The aquatic marsh (AQUAT) was defined as the fully inundated area occurring at the transition between the meadow and the open water and is characterized by a mixture of floating, submergent, and emergent vegetation (see Midwood and Chow-Fraser 2010). Because the marshes were situated in well-defined embayments, the lakeward boundary of the marsh was drawn across the mouth of the embayment. We used this to calculate drainage ratio (DBA/AQUAT). We also determined the width of the opening that connects the marsh to Georgian Bay (OPEN) through which surface water can flow.

Meteorological and water level data

Daily precipitation values were obtained from the Environment Canada weather station in Parry Sound, 20 km north of the study area. These data were used to calculate the cumulative precipitation inputs to catchments over 7-, 14-, and 30-day periods prior to sampling at each marsh. For spring sampling dates, we also used the change in recorded snow depth over these periods to calculate the areal water equivalent and obtain an estimate of the volume of meltwater generated from spring snowpack. We used a snowpack density of 0.35 $g \cdot cm^{-3}$, a value typical for the late spring in south-central Ontario (Logan 1973). The sum of the precipitation inputs and areal water equivalent from the change in snowpack were taken to be the total precipitation and meltwater inputs to the catchment over the 7-, 14-, and 30-day periods (PREC$_{07}$, PREC$_{14}$, and PREC$_{30}$). Lake-level data (averaged over 1-day intervals; LVL) were obtained from the Parry Sound station maintained by the Canadian Hydrographic Services (Parry Sound, Ontario).

Field sampling

Marsh surveying

Sampling surveys were conducted twice in 2009. The first sampling period occurred during the week following ice-out in mid-April, towards the end of the snowmelt period. We were unable to sample Hennessy Bay (HNB) in spring, but all of the other 33 sites were visited at this time. The second round of sampling occurred over a 10-day period in mid-July; this corresponded with conditions of tributary baseflow and the time during which many sampling programs are conducted to assess Great Lakes water quality (e.g., Chow-Fraser 2006; Trebitz et al. 2007; Morrice et al. 2008). Sampling was not undertaken during or within 48 h following notable (>5 mm) rain events. The time of day during which sampling occurred varied from site to site, but fell between the hours of 0830 and 1800.

Samples were collected adjacent to the longest axis of the watershed, near the 0.5 to 1.0 m depth contours, depending on accessibility and site morphology. We sampled at roughly the same locations during spring and summer surveys (locations were marked on a map and global positioning system (GPS) points were taken). Efforts were made not to disturb submerged vegetation. A YSI 6600 multiprobe (YSI, Yellow Springs, Ohio, USA) was used to measure COND and pH in situ. Water samples for nutrient and suspended solids analysis were collected at mid-depth and kept cold until they could be processed or frozen at the end of the day.

Continuous monitoring

Following ice-out in mid-April, an ISCO 6720 automatic water sampler and a YSI 6600 multiprobe were installed at Black Rock marsh (BLR) in Tadenac Bay (Fig. 1). BLR is a 4.7 ha marsh located downstream of a moderately sloped (4.4%), 271.5 ha drainage basin containing 70.1 ha of upstream wetland. Upstream surface waters have low mid-summer pH (5.16–6.45) and COND (3–15 $\mu S \cdot cm^{-1}$) and high TP (11.9–61.9 $\mu g \cdot L^{-1}$) and COL (170–345 mg $Pt \cdot L^{-1}$). The ISCO sampler collected daily water samples in the marsh that were later analysed for COL and TP, and the probe stored hourly measurements of COND and pH. The probe was calibrated in the lab before deployment, and COND and pH were checked and (or) calibrated with standards in the field during site visits (generally every 20–24 days).

Sample processing

Water samples for total ammonia nitrogen (NH_3-N + NH_4^+-N; TAN), total nitrate–nitrite nitrogen (NO_3^--N + NO_2^--N;

Table 3. Landscape characteristics for the 34 sampled marshes.

								PREC$_{avg}$ (m^3)		
Site code	Latitude (°N), longitude (°W)	Aquatic marsh (ha)	Meadow marsh (ha)	Marsh opening (m)	Drainage basin (ha)	Upstream wetland (ha)	Slope (%)	7-day	14-day	30-day
MS1	44.952, 79.851	4.4	1.1	126	15.3	2.0	8.9	801	2 961	13 804
MS2	44.946, 79.894	0.9	0.1	63	122.2	17.8	3.2	6 414	23 700	110 496
CG1	44.952, 79.913	3.6	0.4	107	22.3	0.0	5.9	1 955	9 316	20 208
CG2	44.959, 79.912	3.0	0.6	181	168.0	35.7	4.1	8 823	32 602	152 005
LNB	44.969, 79.895	2.2	4.9	93	496.9	82.0	5.5	26 088	96 403	449 467
LSP	44.979, 79.932	5.5	0.8	94	133.1	29.6	2.5	6 988	25 822	120 393
RDB	44.985, 79.921	4.0	0.9	40	43.1	1.9	5.3	2 264	8 368	39 014
PGI	44.992, 79.926	1.0	0.7	33	26.5	0.0	6.9	1 392	5 145	23 987
RBH	44.994, 79.922	2.6	0.3	63	70.8	12.3	5.8	3 717	13 735	64 037
INB	44.997, 79.922	1.3	4.4	8	262.5	49.0	4.7	13 781	50 923	237 422
PTC	45.005, 79.929	1.5	2.3	79	86.8	0.0	4.5	4 558	16 842	78 523
GHR	45.006, 79.913	0.4	0.8	64	584.4	141.9	5.6	30 682	113 377	528 605
MR1	45.014, 79.944	17.0	10.5	304	476.6	104.7	3.2	25 021	92 457	431 070
MR2	45.012, 79.951	0.9	8.8	179	121.9	0.0	2.0	6 399	23 644	110 239
BRI	45.018, 79.982	2.6	1.5	49	95.6	21.9	2.1	5 019	18 548	86 478
DVB	45.045, 79.999	0.8	0.3	24	15.4	2.0	0.9	1 346	7 132	13 918
TB1	45.028, 79.983	4.7	3.4	56	173.5	31.6	2.9	11 274	79 440	170 154
TB2	45.042, 79.990	1.8	1.0	108	8.4	0.0	0.6	546	3 848	8 243
TB3	45.052, 79.958	0.9	0.2	106	11.9	0.1	1.9	775	5 458	11 690
TB4	45.057, 79.995	0.4	0.2	26	13.7	0.0	3.9	891	6 276	11 915
TL1	45.035, 79.954	2.6	0.2	58	91.6	8.7	2.1	5 953	41 949	89 851
TL2	45.047, 79.914	0.9	0.9	102	274.2	37.3	6.0	17 826	125 602	269 030
THB	45.052, 79.970	1.2	1.0	57	29.8	0.0	0.7	1 936	13 639	29 214
CFR	45.048, 79.988	2.8	2.2	236	82.1	9.7	2.0	5 338	37 615	80 568
BLR	45.043, 79.973	4.7	4.5	26	271.5	70.1	1.8	17 651	124 369	266 390
ALB	45.053, 80.002	1.5	0.9	79	15.6	0.0	4.4	1 012	7 130	15 272
MRB	45.118, 79.978	20.4	13.8	310	354.6	36.8	5.9	22 698	68 980	331 424
WB1	45.138, 80.014	25.6	5.5	257	61.2	1.0	9.7	3 917	11 903	57 190
WB2	45.129, 79.984	3.0	2.5	153	37.9	9.4	7.6	2 426	7 372	35 422
MB1	45.115, 80.017	6.7	1.3	52	141.5	12.9	5.6	9 058	27 526	145 203
MB2	45.113, 80.035	1.9	3.5	147	554.4	102.0	3.8	35 482	107 832	568 822
MB3	45.126, 80.009	1.2	0.3	50	6.8	0.0	8.7	434	1 319	6 339
BLB	45.131, 80.026	1.0	1.9	108	41.2	6.0	5.3	2 638	8 017	42 292
HNB	45.141, 80.041	1.2	0.3	74	66.4	10.3	6.2	4 247	12 906	68 081

Note: Subscript "avg" refers to spring–summer average.

Table 4. Pearson's correlation coefficients for landscape variables (*a*) and for spring–summer-averaged water chemistry variables in coastal marshes (*b*).

(*a*) Landscape variables.

	DBA	WET	SLOPE	AQUAT	MED	OPEN	DBA/AQUAT	PROPWET	$PREC_{07}$	$PREC_{14}$	$PREC_{30}$
DBA	1.00										
WET	**0.88**	1.00									
SLOPE	–0.06	–0.05	1.00								
AQUAT	0.28	0.19	0.22	1.00							
MED	**0.55**	**0.40**	0.06	**0.53**	1.00						
OPEN	0.16	0.16	0.15	**0.48**	**0.36**	1.00					
DBA/AQUAT	**0.72**	**0.67**	–0.22	**–0.47**	0.11	–0.20	1.00				
PROPWET	**0.65**	**0.81**	–0.05	0.19	0.23	0.00	**0.46**	1.00			
$PREC_{07}$	**0.99**	**0.88**	–0.08	0.29	**0.54**	0.17	**0.71**	**0.64**	1.00		
$PREC_{14}$	**0.95**	**0.84**	–0.25	0.22	**0.49**	0.12	**0.71**	**0.59**	**0.95**	1.00	
$PREC_{30}$	**0.99**	**0.88**	–0.06	0.28	**0.55**	0.17	**0.72**	**0.65**	**0.99**	**0.98**	1.00

(*b*) Water chemistry variables.

	TP	SRP	TAN	TNN	SO_4^{2-}	COND	pH	DOC	COL	TSS
TP	1.00									
SRP	0.20	1.00								
TAN	0.22	–0.33	1.00							
TNN	–0.02	–0.19	–0.09	1.00						
SO_4^{2-}	**–0.54**	0.13	**–0.47**	0.29	1.00					
COND	**–0.49**	–0.02	**–0.37**	0.11	**0.86**	1.00				
pH	**–0.40**	–0.09	–0.26	0.19	**0.58**	**0.61**	1.00			
DOC	**0.40**	**0.52**	**–0.38**	–0.18	–0.01	–0.11	–0.19	1.00		
COL	**0.61**	0.05	**0.51**	**–0.40**	**–0.75**	**–0.60**	**–0.48**	0.20	1.00	
TSS	**0.51**	–0.02	**0.40**	–0.10	**–0.44**	**–0.42**	**–0.47**	0.14	**0.54**	1.00

Note: Significant correlations are shown in bold font ($P < 0.05$). Refer to Tables 1 and 2 for definitions of variables.

Table 5. Pearson correlations between landscape variables and water chemistry variables in coastal marshes.

	DBA	WET	SLOPE	AQUAT	MED	OPEN	DBA/AQUAT	PROPWET	PREC_{07}	PREC_{14}	PREC_{30}
TP_{avg}	**0.46**	**0.41**	**0.36**	**0.52**	**0.41**	0.19	0.05	0.27	**0.47**	0.32	**0.46**
SRP_{avg}	0.25	0.24	0.05	0.03	–0.04	-0.07	0.21	0.13	0.24	0.20	0.24
TNN_{avg}	**–0.40**	–0.34	**0.46**	0.15	–0.11	0.20	**-0.48**	–0.25	**–0.40**	**–0.42**	**–0.40**
TAN_{avg}	**0.35**	0.22	0.04	0.29	**0.49**	**0.49**	0.11	0.07	**0.37**	**0.36**	**0.36**
$\mathrm{SO_4^{2-}}_{avg}$	**–0.61**	**–0.55**	0.02	–0.20	**–0.43**	-0.10	**-0.42**	**–0.38**	**–0.64**	**–0.62**	**–0.63**
COND_{avg}	**–0.60**	**–0.54**	–0.14	–0.22	–0.28	-0.24	**-0.39**	–0.32	**–0.62**	**–0.60**	**–0.60**
pH_{avg}	**–0.67**	**–0.57**	–0.28	0.02	–0.31	-0.09	**-0.63**	**–0.46**	**–0.63**	**–0.54**	**–0.66**
DOC_{sp}	0.00	0.06	–0.17	–0.06	–0.24	-0.24	0.04	0.11	–0.10	–0.03	0.00
DOC_{su}	**0.38**	**0.46**	0.22	0.10	0.00	0.04	0.28	**0.44**	**0.49**	0.27	**0.35**
DOC_{avg}	0.19	0.28	0.01	0.00	–0.16	-0.13	0.18	0.29	0.16	0.10	0.18
COL_{avg}	**0.63**	**0.58**	–0.15	0.25	**0.53**	0.16	**0.40**	**0.45**	**0.66**	**0.63**	**0.63**
TSS_{avg}	**0.50**	**0.43**	0.28	0.30	**0.46**	**0.37**	0.28	**0.49**	**0.50**	**0.37**	**0.49**

Note: Significant correlations are shown in bold font ($P < 0.05$). Subscript terms indicate the following: sp, spring; su, summer; avg, spring–summer average.

Table 6. Pearson correlations of landscape variables with the first two principal component axes ($n = 34$).

Axis	Variance explained (%)	Variable	r
PC1	47.7	DBA	0.97
		PREC_{07}	0.97
		WET	0.94
		PROPWET	0.77
		DBA/AQUAT	0.69
		MED	0.58
PC2	23.5	AQUAT	0.86
		OPEN	0.70
		DBA/AQUAT	–0.63
		MED	0.53
		SLOPE	0.43

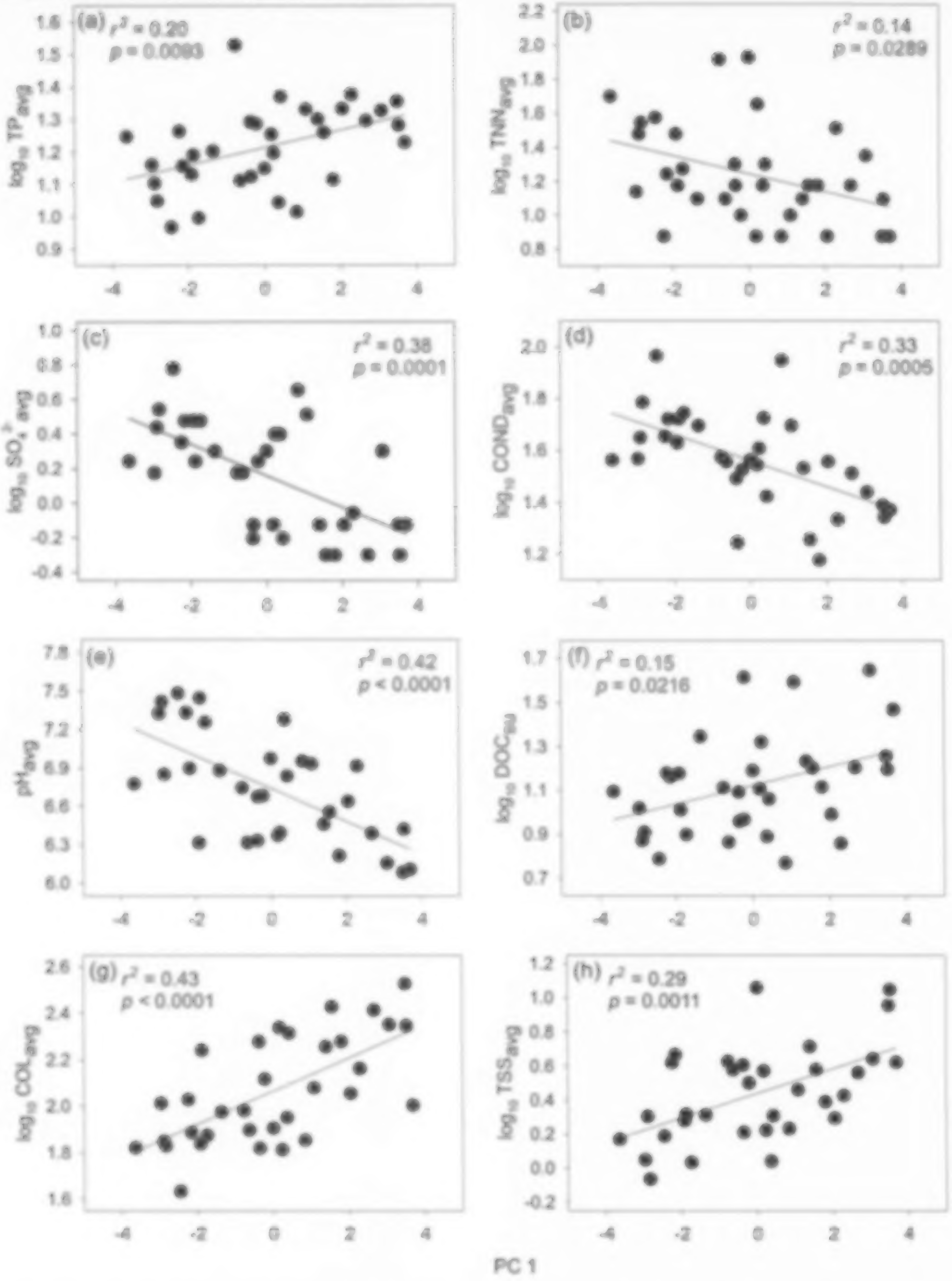
TNN), COL, and $\mathrm{SO_4^{2-}}$ were processed on the day of collection with a Hach DR/890 colorimeter and Hach reagents and protocols. During this time, samples for TSS were also filtered through preweighed 0.45 µm GF/C filters, which were frozen until subsequent analysis. Filtrate was split, and a portion was frozen and stored for later analysis of soluble reactive phosphorus (SRP) content. A second portion was acidified with nitric acid (to a pH < 2) and refrigerated at 4 °C for later analysis of DOC content. Raw water samples were frozen and stored for TP analyses.

During laboratory processing, TP samples were digested using persulfate in an autoclave. SRP samples (undigested) and digested TP samples were then analysed according to the molybdenum blue method (Murphy and Riley 1962), with absorbance readings taken on a Genesys spectrophotometer. TSS filters were dried in a drying oven at 100 °C for 1 h, placed in a desiccator for 1 h, and weighed. Preserved DOC samples were analysed with the NPOC method in a Shimdzu TOC–VCHP analyser.

Data analyses and statistics

Statistical analyses were performed in SAS JMP 7.0 (SAS Institute Inc., Cary, North Carolina), with $\alpha = 0.05$. $\mathrm{SO_4^{2-}}$, TAN, and TNN values that fell below the detection limit ($1\ \mathrm{mg{\cdot}L^{-1}}$, $10\ \mathrm{\mu g{\cdot}L^{-1}}$ and $10\ \mathrm{\mu g{\cdot}L^{-1}}$, respectively) were assigned half the detection limit value, a technique commonly used to treat data with concentrations below detection (e.g., Trebitz et al. 2007). Variable data with non-normal distributions were $\log_{10}$- or square-root-transformed as appropriate, with the exception of water level, for which it was necessary to square the data. Spring TSS for WB1 was excluded because strong winds on the morning of collection resulted in an unusually high value. We used Pearson correlation matrices to examine relationships among landscape variables and among water chemistry variables. Pearson correlation was also used in initial examination of bivariate relationships between landscape and water chemistry variables. Spring–summer averages of water chemistry variables at each surveyed site were used with the exception of DOC; we used summer DOC because preliminary analyses revealed that only summer concentrations were significantly related to landscape variables. In the case of BLR, data used in these analyses were from discrete samples taken during the same

Figure 2. Plots of water chemistry variables against landscape PC1 (su, summer; avg, spring–summer averaged concentrations). Only variables with statistically significant relationships to PC1 are shown.



spring and summer sampling periods as the other 33 marshes.

Because of multicollinearity among landscape variables, we used two statistical methods to aid interpretation of relationships between landscape and water chemistry variables. First, we conducted a principal components analysis (PCA) using a correlation matrix to condense transformed landscape variables (Table 2) into synthetic axes that best explain the variation (Shaw 2003). Since all precipitation measures were highly correlated with each other, we used only the averaged 7-day cumulative precipitation and snowmelt inputs in the PCA. Axes with an eigenvalue greater than one were retained

Table 7. Models built from forward stepwise regressions.

Parameter	n	Equation	r^2 [a]	r^2_{adj}
$\log_{10}$ COND$_{avg}$	33	$2.320 - 0.208\log_{10}(\mathrm{PREC}_{07avg})^{***}$	0.38	0.36
$\log_{10}$ SO$_4^{2-}{}_{avg}$	33	$1.505 - 0.369\log_{10}(\mathrm{PREC}_{07avg})^{****}$	0.41	0.39
pH$_{avg}$	33	$8.023 - 0.263\log_{10}(\mathrm{DBA})^{*} - 0.0711(\mathrm{SLOPE})^{**} - 0.317\log_{10}(\mathrm{DBA/AQUAT})^{**}$	0.44, 0.55, 0.64	0.61
$\log_{10}$ COL$_{avg}$	33	$1.062 + 0.275\log_{10}(\mathrm{PREC}_{07avg})^{****}$	0.43	0.41
$\log_{10}$ TSS$_{avg}$	33	$-0.718 + 0.270\log_{10}(\mathrm{PREC}_{07avg})^{**} + 0.0398(\mathrm{SLOPE})^{*}$	0.25, 0.36	0.32
$\log_{10}$ TP$_{avg}$	33	$0.770 + 0.0956\log_{10}(\mathrm{AQUAT})^{*} + 0.0926\log_{10}(\mathrm{PREC}_{07avg})^{**} + 0.0166(\mathrm{SLOPE})^{*}$	0.28, 0.39, 0.48	0.42
$\log_{10}$ TNN$_{avg}$	33	$1.333 - 0.188\log_{10}(\mathrm{DBA/AQUAT})^{*} + 0.0451(\mathrm{SLOPE})^{*}$	0.23, 0.35	0.31
$\log_{10}$ TAN$_{avg}$	33	$0.573 + 0.307\log_{10}(\mathrm{OPEN})^{*} + 0.191\log_{10}(\mathrm{MED})^{*}$	0.24, 0.36	0.31
$\log_{10}$ DOC$_{su}$	34	$0.520 + 0.173\log_{10}(\mathrm{PREC}_{07su})^{**}$	0.24	0.21

Note: Subscript terms indicate the following: su, summer; avg, spring–summer averaged. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

[a] Cumulative for each variable entered.

for further analysis. We interpreted principal component (PC) axes by using Pearson correlation to examine the strength of the relationships between the landscape variables and each retained PC axis. We then regressed water chemistry variables against PC site scores. This technique allowed us to focus on the shared contributions of all explanatory variables (Graham 2003). Secondly, we used the landscape variables in forward stepwise multiple regression analyses to generate explanatory models for water chemistry variables. Only variables having statistically significant effects were retained in the models.

To look for seasonal variation, we used paired *t* tests to determine whether water chemistry variables differed in their concentrations between spring and summer surveys and also to look for differences in the precipitation and snowmelt inputs to the catchments during the two periods. We used the continuous data from Black Rock marsh to further examine seasonal variation in water chemistry in relation to hydrology. This was accomplished by using forward stepwise multiple regressions (in the same manner as above) to determine the effects of day of year, lake level, and precipitation and snowmelt inputs on daily averages of total phosphorus, colour, specific conductivity, and pH.

Results

Landscape and water chemistry characteristics

Watersheds ranged broadly in size from 6.8 ha (MB3) to 584.4 ha (GHR), with a mean of 146.4 ha (Table 3). Several of the smaller watersheds did not contain any upstream wetland, while GHR, MR1, and MB2 each contained over 100 ha of wetland upstream of the marsh. Typical of other regions in Georgian Bay, most aquatic marshes in this study were smaller than 10 ha in size, with the exceptions of MR1, MRB, and WB1. Mean watershed slope ranged from 0.6% (TB2) to 9.7% (WB1), with an average of 4.4%. There was considerable collinearity among landscape variables, with the strongest correlations occurring between DBA and measurements of precipitation and snowmelt inputs to catchments (Table 4*a*).

Compared with the offshore, water in coastal marshes was high in TP, SRP, TAN, TSS, COL, and DOC (group 1; Table 1) and low in pH, COND, TNN, and SO_4^{2-} (group 2). Variables in group 1 were positively correlated with each other and negatively correlated to variables in group 2 (Table 4*b*). The strongest relationships were between COND and each of SO_4^{2-} ($r = 0.86$), pH ($r = 0.61$), and COL ($r = -0.60$) and between COL and each of TP ($r = 0.61$) and SO_4^{2-} ($r = -0.75$). Although spring–summer-averaged DOC was not significantly correlated with COL, summer concentrations of DOC and COL were significantly positively correlated with each other ($r = 0.48$, $P = 0.0038$).

Pearson correlations revealed several trends in relationships between landscape and water chemistry variables (Table 5). Averaged concentrations of COND, SO_4^{2-}, pH, COL, TSS, and often TP were generally correlated to the same set of landscape variables, with many of these variables showing the strongest relationships to drainage basin area and precipitation and snowmelt inputs; correlations were positive for variables measuring loading (TSS, TP, COL) but negative for variables measuring ionic strength (pH, COND, SO_4^{2-}).

Table 8. Comparison of spring and summer means (and ranges) of precipitation and snowmelt inputs to catchments and of water chemistry variables using paired *t* tests (NS, not significant).

Parameter	Spring	Summer	*t*	*P*
Precipitation and snowmelt inputs to catchments				
$PREC_{07}$ (m^3)	4 902 (534–57 104)	2 992 (170–40 909)	–2.78	0.0089
$PREC_{14}$ (m^3)	27 746 (1 438–202 664)	9 935 (1 201–98 130)	–11.69	<0.0001
$PREC_{30}$ (m^3)	84 762 (8 269–675 822)	53 715 (4 409–461 821)	–23.65	<0.0001
Water chemistry parameters				
TP ($\mu g \cdot L^{-1}$)	15.2 (8.4–44.3)	17.1 (10.2–28.8)	1.92	NS
SRP ($\mu g \cdot L^{-1}$)	5.5 (1.5–15.8)	4.4 (1.3–10.7)	–2.04	0.0494
TAN ($\mu g \cdot L^{-1}$)	11 (5–40)	16 (5–160)	2.11	0.0427
TNN ($\mu g \cdot L^{-1}$)	23 (10–120)	11 (5–50)	–6.57	<0.0001
SO_4^{2-} ($mg \cdot L^{-1}$)	1.0 (0.5–5.0)	1.7 (0.5–7.0)	3.56	0.0012
COND ($\mu S \cdot cm^{-1}$)	26 (8–74)	45 (15–114)	6.95	<0.0001
pH	6.8 (5.8–8.1)	7.0 (6.2–8.2)	1.31	NS
DOC ($mg \cdot L^{-1}$)	18.5 (7.4–97.0)	13.2 (5.9–44.3)	–3.08	0.0042
COL (mg $Pt \cdot L^{-1}$)	120 (65–250)	103 (11–424)	–1.41	NS
TSS ($mg \cdot L^{-1}$)[a]	2.5 (0.7–20.0)	2.5 (0.7–17.1)	0.10	NS

[a] WB1 excluded.

Both TP and TNN were positively related to watershed slope, and TP was also positively related to size of the aquatic marsh. Summer DOC showed positive relationships to DBA, PREC, and upstream wetland variables (WET and PROPWET), whereas spring and averaged DOC and SRP concentrations were not significantly related to any of the landscape variables examined.

Landscape principal components

PCA on landscape variables yielded two axes with eigenvalues greater than one, together explaining 71.2% of the variation in the data set (Table 6). PC1 explained 47.7% of the variation in the data and was highly positively correlated with DBA, $PREC_{07}$, WET, PROPWET, and DBA/AQUAT and weakly correlated with MED. High scores on PC1 are therefore interpreted as marshes that drain large watersheds with large areas of upstream wetland and that receive high precipitation inputs. PC2 explained an additional 23.5% of the variation and showed strong positive correlations with AQUAT and OPEN, a strong negative correlation with DBA/AQUAT, and weak positive correlations with MED and SLOPE; high PC2 scores are therefore most strongly associated with large, open marshes.

PC1 was strongly related to several water chemistry variables; it was positively related to TP, COL, and TSS and to summer DOC and negatively related to TNN, SO_4^{2-}, COND, and pH (Fig. 2). It also showed a weak positive relationship with TAN concentrations ($r^2 = 0.12$, $P = 0.0494$). PC2 was not as strongly related to water chemistry variables; however, it was significantly positively related to TP ($r^2 = 0.16$, $P = 0.0216$), TAN ($r^2 = 0.13$, $P = 0.0397$), and TNN ($r^2 = 0.13$, $P = 0.0368$).

Stepwise regression models using landscape variables

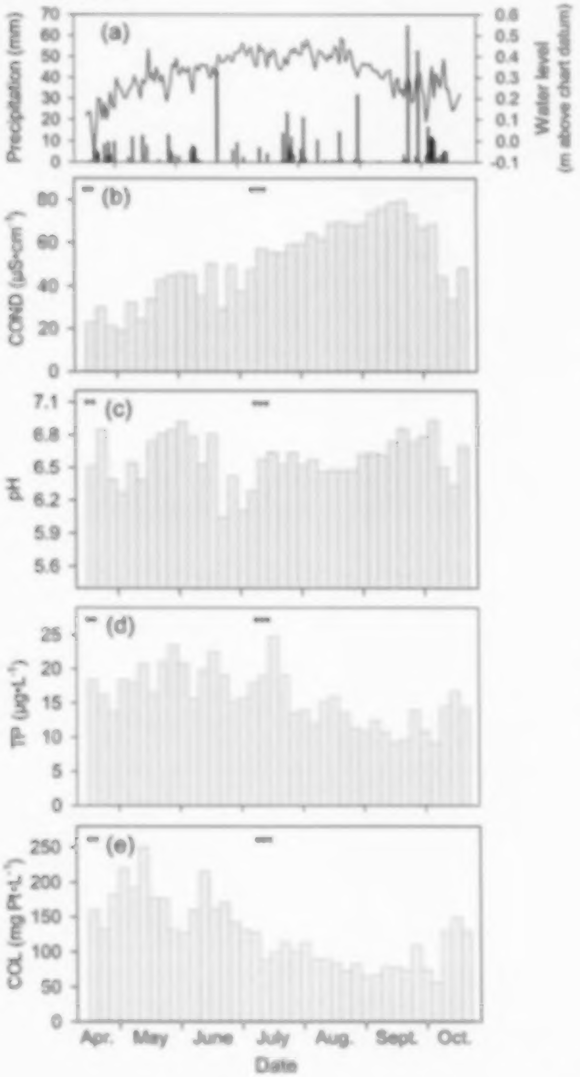
Stepwise regressions identified sets of factors that can best explain the variation in water chemistry variables (Table 7). Landscape variables explained the most variation (64%) in pH; of this, DBA alone explained 44%. $PREC_{07}$ was first to enter the models for COND, COL, TSS, TP, SO_4^{2-}, and summer DOC. In the cases of COND, SO_4^{2-}, COL, and DOC_{sum}, no other landscape variables had significant effects. Drainage slope had significant effects for several variables, including TSS, TP, and TNN (positive relationships) and pH (negative relationship). Size of the aquatic marsh also entered the model for TP. Unlike other chemistry variables, TAN was most closely related to marsh-level variables; MED and OPEN together explained 36% of variation in averaged TAN concentrations.

Seasonal patterns in marsh water chemistry

Total precipitation and snowmelt inputs to catchments over 7-, 14-, and 30-day periods leading up to sampling were all significantly higher in spring than summer, largely due to contributions from snowmelt in spring (paired *t* tests; Table 8). TP, pH, COL, and TSS did not differ significantly between the April and July sampling periods when all sites were considered (paired *t* tests; Table 8). Mean SRP, TNN, and DOC concentrations were all lower in the summer compared with spring, with TNN showing the largest and most significant decline (from 23 to 11 $\mu g \cdot L^{-1}$). TAN, SO_4^{2-}, and COND were all significantly higher during the summer; mean COND concentrations showed the greatest increase, from 26 $\mu S \cdot cm^{-1}$ in spring to 45 $\mu S \cdot cm^{-1}$ in summer.

Consistent with the broader surveys, continuous monitoring at Black Rock marsh revealed an increase in COND throughout the spring and summer, from around 20 $\mu S \cdot cm^{-1}$ in mid-April to nearly 80 $\mu S \cdot cm^{-1}$ in late summer, before declining in early fall (Fig. 3). Stepwise regression models showed that COND was positively related to day of year and water level and negatively related to $PREC_{30}$; together, these variables explained 69% of the variation in COND (Table 9). Water pH fluctuated between 6.1 and 6.9 throughout the monitoring period and was not significantly related to day of year, water level, or PREC. TP ranged between 14 and 25 $\mu g \cdot L^{-1}$ during the months of April to July, after which it began to decline; the lowest 5-day averaged concentration was 9 $\mu g \cdot L^{-1}$ in early October. Day of year was the only variable to enter the model for TP (negative relationship), explaining

Figure 3. Trends in key water chemistry variables at Black Rock marsh from mid-April to mid-October. Asterisks were used to indicate timing of discrete sampling surveys across all marshes. Panel (*a*) shows daily precipitation (bars) and water level (line) during the study period.



32% of the variation in daily concentrations. COL was highest in spring (up to 250 mg Pt·L^{-1}), and declined in summer and early fall to a low of around 56 mg Pt·L^{-1} in early October. Both day of year and water level entered the model for COL (negative relationships), together explaining 49% of the variation.

Discussion

Watershed runoff versus Georgian Bay water

Marshes examined in our study lie at the transition between Precambrian Shield watersheds and Georgian Bay and represent areas of unique water chemistry due in large part to the unique geological setting. Precambrian Shield watersheds export large quantities of sediment, DOC, phosphorus, and colour to downstream surface waters (Gergel et al. 1999; Dillon and Molot 2005; Eimers et al. 2008). Catchment soils and wetlands also tend to retain a large portion of atmospherically derived nitrate (Devito et al. 1989; Dillon and Molot 1990), and under some conditions (e.g., sustained high water table) can retain sulphate (Devito 1995). Consequently, runoff tends to be highly coloured, acidic, and relatively phosphorus-rich, but low in dissolved ions (Allan et al. 1993). By contrast, the sedimentary bedrock that underlies the majority of Great Lakes watersheds, including the southern and western portion of Georgian Bay, results in relatively alkaline, well-buffered lake water. Compared with runoff from the crystalline Shield rock, Georgian Bay water is low in phosphorus, but is a relatively rich source of dissolved ions, including sulphate and nitrate, and has a high pH. The resulting gradation in water chemistry from land to water in eastern Georgian Bay results in distinct patterns in water chemistry (groupings of watershed- vs. lake-derived variables).

Landscape influences on marsh water chemistry

We found that larger drainage basins tended to contain more upstream wetland both in terms of absolute area and as a proportion of the total watershed and received higher precipitation and snowmelt inputs. Thus, marshes were ordinated along a gradient related to degree of watershed influence, that is, potential to generate runoff that is subject to land-based processes such as nutrient and ion uptake, transformation, and release in soils and wetlands (Devito et al. 1989; Allan et al. 1993). Sites with larger watershed influence (higher PC1 scores) had higher concentrations of TP, COL, TSS, TAN, H$^+$, and DOC, but lower concentrations of COND, TNN, and SO_4^{2-}. Since PCA could not elucidate the degree to which watershed size alone versus other factors (e.g., precipitation and snowmelt inputs or amount of upstream wetland) influenced water chemistry, we relied on the relative strength of each independent variable in regression analyses to provide further insight.

Stepwise regressions identified precipitation and snowmelt inputs to catchments (the product of drainage area and precipitation + snowmelt) as the strongest predictor of the majority of marsh water chemistry variables, including SO_4^{2-}, COND, TP, COL, TSS, and summer DOC, while drainage area was the strongest predictor of pH. Previous studies on inland lakes have found drainage area to have a strong influence on nutrient and sediment loadings; TSS, DOC, and COL largely originate from terrestrial sources, thus larger watersheds tend to produce higher loadings to downstream waters (Curtis and Schindler 1997; Dillon and Molot 2005; Eimers et al. 2008). Similarly, a positive relationship between TP and watershed size is attributed to the fact that a larger drainage area theoretically results in higher P loading because of weathering and atmospheric deposition (Schindler 1971). Our finding that water chemistry variables showed a stronger relationship to short-term (7-day) precipitation and snowmelt inputs to catchments than to drainage area alone demonstrates that hydrologic flushing has a dominant role in export of catchment-derived constituents to downstream marshes. Additionally, higher precipitation and

Table 9. Models built from forward stepwise regressions for seasonal water chemistry data at Black Rock marsh.

Parameter	n	Equation	r^2 [a]	r^2_{adj}
$\log_{10}$ COND	187	$-0.0787 + 0.00256\text{DATE}^{****} - 0.346\log_{10}(\text{PREC}_{30})^{****} + 0.831(\text{LVL})^{2****}$	0.49, 0.63, 0.69	0.68
$\log_{10}$ COL	187	$2.584 - 0.00215\text{DATE}^{****} - 0.850(\text{LVL})^{2****}$	0.42, 0.49	0.48
$\log_{10}$ TP	187	$1.457 - 0.00137\text{DATE}^{****}$	0.32	0.32

Note: ****, $P < 0.0001$.

[a] Cumulative for each variable entered.

snowmelt inputs to catchments tends to result in higher discharge (Yao et al. 2008; Buttle and Eimers 2009), which can reduce the seiche-induced inflow of lake water to a marsh (Trebitz et al. 2002). Consequently, marshes with high measures of PREC_{07avg} tended to have lower water pH, COND, TNN, and SO_4^{2-} concentrations because of reduced buffering and ionic loadings from the lake.

Other factors may also affect the amount of lake water influence in a marsh. The openings to several of the marshes in our study occurred within larger shoreline embayments, which themselves experience varying degrees of mixing with the offshore water. Thus, examining the position of marshes in relation to broader shoreline morphology would likely account for some additional variation in water chemistry characteristics, as would examining the degree of site-to-site variation in seiche amplitude (see Trebitz et al. 2002). In addition, the opening width that connects the marsh to the lake may influence the amount of mixing that occurs via longshore currents; however, we did not find evidence of this effect in our study, possibly owing to the presence of overriding factors.

While summer DOC was best explained by 7-day precipitation and snowmelt inputs to catchments and also showed a moderately strong relationship to area of upstream wetland, spring DOC was not significantly related to landscape variables. This may be partly a result of variation in the seasonality of sources of DOC. Wetlands are widely reported to be a major source of DOC to downstream waters during runoff events (Dillon and Molot 1997; Kothawala et al. 2006; Eimers et al. 2008), and DOC production and leaching from peat is highest during summer months (Hongve 1999). Variation in spring concentrations, however, may be largely a function of catchment variables not examined in our study, such as the area of deciduous forest cover; deciduous leaf litter can be a major source of DOC between autumn and spring thaw (Hongve 1999). Some research also indicates that distinguishing among wetland types may have yielded stronger relationships between upstream wetland variables and water chemistry variables (including DOC), since young beaver ponds often have a different effect on runoff chemistry than do mature swamps and fens (Devito et al. 1989; Kothawala et al. 2006).

Slope contributed significantly to explanatory models for TNN, TP, TSS, and pH, with positive relationships with each variable except pH. A positive relationship between TNN levels and slope of the drainage basin has also been observed in other freshwater systems of the Precambrian Shield (Dillon et al. 1991; D'Arcy and Carignan 1997); it has been hypothesized that in steeper catchments, fewer areas with saturated soils develop during high runoff, resulting in less opportunity for denitrification and assimilation of nitrate in upper soil horizons (D'Arcy and Carignan 1997). Similarly, less development of anoxic soil conditions in steep catchments can explain the negative relationship between slope and pH. Consistent with our findings, Dillon et al. (1991) found a positive relationship between TP export in Precambrian Shield streams and catchment slope, even though it was not statistically significant. By contrast, D'Arcy and Carignan (1997) found a negative relationship, which they attributed to less opportunity for export of dissolved P in steep catchments. Our observation of higher concentrations of TSS in marshes with steeper catchments makes us more confident about a positive relationship, and we suggest that increased sediment export from steep slopes may provide a mechanism for greater export of sediment-bound P to downstream marshes.

Marsh-level variables were generally only weakly related to water chemistry variables. Landscape PC2 ordered marshes along a gradient where high scores corresponded to large, open marshes; this axis was weakly positively related to TP, TNN, and TAN. While the mechanism behind these relationships is not clear, we speculate that the finding of higher nutrient levels in large marshes may be related to the storage and release of these nutrients in marsh sediments and organic matter (Bowden 1987; Craft et al. 1989). Marshes in our study generally support dense submerged aquatic vegetation that can filter and cause settling of organic and inorganic particulate matter entering from the watershed and can also play a role in the transfer of nutrients between sediments and the water column (Nichols 1983). Detailed bathymetric information would have allowed us to estimate residence times, which could have explained additional variation in some water-chemistry parameters; however, digital elevation models for such remote locations do not currently exist.

Seasonal trends in marsh water chemistry

Knowledge of seasonal variation in marsh water chemistry is important in temperate coastal areas, where snowmelt plays a major role in water and nutrient budgets (Barica and Armstrong 1971). Past studies examining seasonal patterns in coastal marsh water chemistry are few and tend to be limited to single-site observations (e.g., Mitsch and Reeder 1992; Morrice et al. 2004). During spring, snowmelt results in high hydrologic flow from watersheds, and this can increase runoff contribution and reduce the influx of lake water into coastal bays and wetlands (Trebitz et al. 2002; Morrice et al. 2004). Spring runoff from Precambrian Shield catchments delivers large quantities of DOC, colour, and P to downstream waters (Dillon and Molot 2005; Eimers et al. 2008), but is not a major source of dissolved ions, nitrates, and sulphates (Allan et al. 1993). Consistent with these studies, we found higher concentrations of DOC and SRP in April than in July surveys and a continued decline in TP and colour during the late summer and early fall at Black Rock marsh; together, these results indicate higher loadings of catchment-derived constituents during spring and early summer.

In contrast with the spring scenario, influx of lake water into coastal wetlands is generally highest during summer, when tributaries are at baseflow (Trebitz et al. 2002; Morrice et al. 2004). Georgian Bay water represents a source of conductivity, alkalinity, nitrates, and sulphates to coastal marshes. While nitrates may be used up rapidly in these carbon-rich systems through biotic processes of assimilation and denitrification (Bowden 1987), particularly in the marsh – lake water mixing zone (Morrice et al. 2004), sulphates are less readily reduced in the presence of nitrates (Whitmire and Hamilton 2005), and specific conductivity is also relatively conservative (Cox et al. 2007). Thus, increased inflow of lake water likely contributes to the increase in dissolved ions (higher specific conductivity and SO_4^{2-} concentrations) during summer. Higher rates of evapotranspiration and increased amounts of runoff in the form of shallow groundwater rather than overland flow may also contribute to the seasonal variation in specific conductivity.

At Black Rock marsh, lake level had a significant effect on daily fluctuations in COND and COL, whereby COL decreased and COND increased with an increase in lake level. This may indicate that seiche-induced inflow of lake water acts to dilute runoff and increase ionic loadings to the marsh; however, frequent (e.g., hourly) measurements of in-marsh water level and water chemistry through the duration of a seiche cycle would be necessary to provide a clearer understanding of the magnitude of seiche-induced influences on water chemistry of these marshes (see Morrice et al. 2004). Since tributaries in the study area tend to have very low conductivity (<10 μS·cm^{-1}) relative to the lake, increased hydrologic flows from the watershed following rain events likely contributed to the negative relationship between $PREC_{10}$ and COND at Black Rock marsh.

In addition to watershed and lake influxes, seasonal changes in bioavailable nutrients are influenced by internal marsh processes. Rates of biogeochemical reactions are generally higher in summer, when temperatures are high and biological activity is at its peak (Mitsch and Reeder 1992; Spieles and Mitsch 2000). Although lake water potentially acts as a major source of nitrate during summer, there are high rates of biotic assimilation and denitrification that can reduce TNN concentrations relative to springtime levels (Bowden 1987; Morrice et al. 2004). Meanwhile, increased organic matter mineralization during the summer may increase production of ammonium (Bowden 1987), contributing to higher summer TAN concentrations. TP in the marshes was not significantly different between April and July, but lower SRP in the water column in July suggests more P was tied up in organic forms at this time; this trend has also been observed in Old Woman Creek in Lake Erie (Mitsch and Reeder 1992). The decrease in TP at Black Rock marsh later in summer and early fall suggests either net P export from the marsh to the Bay or sequestration of P in marsh sediments (e.g., through senesce of plankton; Nichols 1983). Further research is required to first verify the generality of this trend and then determine causality.

Implications

Eastern Georgian Bay is one of the few areas in the Great Lakes where it remains possible to study water chemistry in relation to natural watershed dynamics while establishing true baseline conditions against which future impacts can be assessed. Within a landscape ecology framework, our study draws on knowledge of hydrology and biogeochemistry of Precambrian Shield catchments, and of coastal hydrology and nutrient dynamics, to interpret observed patterns in water chemistry of coastal marshes. In doing so, we have contributed a better understanding of the factors controlling reference chemistry of these ecosystems, something that is of recognized importance in the field of ecosystem conservation and management. The relationships established will be useful for identifying areas that could have high sensitivity to watershed disturbances. For example, our results strongly suggest that marshes with large, steeply sloped watersheds would be more sensitive to intensive land development that adds nutrients or promotes soil erosion in their watershed, and that these detrimental effects may be most evident in spring or following periods of high precipitation, when marsh water concentrations of catchment-derived constituents are highest. Future climate change will likely affect the timing and magnitude of nutrient and ion loadings to these marshes because of anticipated changes in precipitation and runoff patterns throughout the Great Lakes region; the majority of climate change models predict overall dryer catchments around Lake Huron and less snowfall and snowpack accumulation because of more winter precipitation falling as rain (Mortsch and Quinn 1996; Lofgren et al. 2002). As knowledge of coastal wetland dynamics continues to advance, we will become better equipped to manage these valuable habitats and predict and prevent the detrimental effects of human stressors and climate change impacts.

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An age- and sex-structured assessment model for American eels (*Anguilla rostrata*) in the Potomac River, Maryland

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Abstract: American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) populations have declined since the 1980s prompting concern about their status and the causes of decline, but stock assessment approaches to estimate effects of fishing on these populations are lacking. Since 1964, 16% of United States commercial American eel harvest came from the Potomac River, yet American eel abundance, production, and fishing mortality is poorly understood in this system. We developed an age- and sex-structured assessment model for 1980–2008 and compared results with the $F_{50\%}$ biological reference point (BRP). The model included natural mortality, fishing mortality, and sex- and age-specific maturation mortality and selectivity. Between 1980 and 2008 estimated recruitment, biomass, and abundance decreased 82%–89%. In all years since 1993, the exploitation rate exceeded the $F_{50\%}$ BRP. The model was moderately sensitive to changes in natural mortality, standard deviation for fishery and recruitment catch-per-unit-effort indices, and initial fishing mortality. The multidecadal decline in recruitment in Chesapeake eels matches those reported elsewhere for American and European eels, suggesting large-scale processes have affected anguillid eel recruitment in the North Atlantic.

Résumé : Les populations d'anguilles d'Amérique (*Anguilla rostrata*) et d'Europe (*Anguilla anguilla*) ont décliné depuis les années 1980, ce qui a généré des préoccupations sur leur statut et les causes de leur déclin; il n'existe, néanmoins, pas d'études d'évaluation des stocks pour estimer les effets de la pêche sur ces populations. Depuis 1964, 16 % de la récolte commerciale américaine d'anguilles d'Amérique s'est faite dans le fleuve Potomac, bien que l'abondance, la production et la mortalité due à la pêche dans ce système restent mal comprises. Nous avons mis au point un modèle d'évaluation structuré d'après l'âge et le sexe pour 1980–2008 et comparé nos résultats aux points de référence biologiques (BRP) $F_{50\%}$. Le modèle inclut la mortalité naturelle, la mortalité due à la pêche, ainsi que la mortalité reliée à la maturation et la sélectivité spécifiques à l'âge et au sexe. Entre 1980 et 2008, le recrutement, la biomasse et l'abondance estimés ont décru de 82–89 %. Au cours de toutes les années depuis 1993, le taux d'exploitation a dépassé le BRP $F_{50\%}$. Le modèle est modérément sensible aux changements dans la mortalité naturelle, la déviation standard dans les indices des pêches et de capture par unité d'effort du recrutement et la mortalité initiale de la pêche. Le déclin sur plusieurs décennies du recrutement des anguilles dans la baie de Chesapeake correspond à ceux signalés ailleurs pour les anguilles d'Amérique et d'Europe, ce qui laisse croire que des processus à grande échelle affectent le recrutement des anguilles de la famille des Anguillidae dans l'Atlantique Nord.

[Traduit par la Rédaction]

Introduction

American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) populations have decreased substantially since the 1980s (Casselman 2003; Dekker 2003), such that there is considerable concern about their conservation (United States Fish and Wildlife Service 2007; MacGregor et al. 2008). In 2004 the Ontario government closed the American eel commercial fishery for all of Ontario, including Lake Ontario and portions of the St. Lawrence River (MacGregor et al. 2008), and in 2008 American eel was designated as an endangered species in that system (MacGregor et al. 2009). Speculation about the causes of population decline centers on diminished recruitment, disease and parasitism, overharvest, and habitat degradation (Haro et al. 2000). Testing these alternative hypotheses is complicated by the American eel's wide distribution and lack of population structure throughout its range (i.e., panmixia; Tesch 1977). Regional effects (overfishing, habitat degradation, turbine mortality) may not be closely tied to range-wide population consequences be-

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cause local recruitment is probably not related to local spawner abundance (Tesch 1977; Avise 2003; Wirth and Bernatchez 2003). However, given American eel life history, regional sources of mortality should have cumulative consequences on range-wide spawner abundance (MacGregor et al. 2009).

American eels are semelparous with a complex life history, which complicates typical approaches for assessing stock status and developing reference points for fishery management. American eels inhabit coastal and inland brackish and freshwater systems from Greenland to Venezuela (Tesch 1977; Helfman et al. 1987). The American eel population is thought to be panmictic based on life history and genetic evidence (Williams et al. 1973; Williams and Koehn 1984; Avise 2003). Adult (silver) eels from throughout their range migrate to the Sargasso Sea to spawn; those from the farthest reaches of their range migrate thousands of kilometres to spawning grounds. Leptocephalus larvae drift on currents for about 1 year until reaching the continental waters of South, Central, and North America (Helfman et al. 1987; McCleave et al. 1987). Upon reaching shelf waters, leptocephali metamorphose into juvenile-stage, unpigmented glass eels (see Atlantic States Marine Fisheries Commission 2000 for definition of life history stages). As pigmentation develops, the young eels are termed elvers and make their way into bays, rivers, and estuaries. Elvers, once fully pigmented, are termed yellow eels (Tesch 1977). The yellow eel stage is the primary feeding and growth phase for the eel. After approximately 3 to 30+ years (Jessop 1987), the eels mature into nonfeeding adults called silver eels (Tesch 1977).

A recently proposed management tactic for anguillid eels matches regional anthropogenic effects like fishing mortality with regional productivity (International Council for the Exploration of the Sea 2006; Bark et al. 2007; Robinet et al. 2007). Sustainably managing all subcomponents of a population as independent stocks is robust to the underlying source–sink population dynamics (Tuck and Possingham 2000; Wilberg et al. 2008). Until population-wide management can be coordinated, individual regions should manage harvest and other anthropogenic mortality sources at locally sustainable levels. Here we develop an age- and sex-structured assessment (ASSA) model for an American eel stock occurring in the Potomac River region, Chesapeake Bay (Fig. 1) and evaluate whether regional harvests are sustainable based upon best estimates of regional spawner production.

Despite the recent attention American eel has received, few population models exist (e.g., De Leo and Gatto 1995), and relatively little is known about American eel production and abundance. Most commonly used stock assessment models have been developed for iteroparous species with well-defined population structure. These models are not well suited to American eel because American eels are semelparous with overlapping generations, panmictic with a common spawning ground in the Sargasso Sea such that local recruitment is probably not related to local stock size, and catadromous with extremely little data from the oceanic portion of their life cycle that would indicate the size of the spawning stock. Additionally, American eel are relatively data-poor; although data collection is improving, there are almost no fishery-independent indices of abundance, length composition or age structure of the harvest, or maturation or sex ratio data available for most of the American eel range (Electric Power Research Institute 1999). We have developed a stock assessment model that requires relatively little data but can be applied to American eel and many other anguillid eel species because it explicitly models American eel's semelparous life history and does not include assumptions about a stock–recruitment function.

Our goal was to estimate the effect of fishing on American eel and develop fishing mortality biological reference points (BRP) to aid in management of the fishery. To address these objectives, we applied the ASSA model to the Potomac River eels using fishery-dependent catch and effort data, demographic data collected in 2007, and a fishery-independent index of recruitment. The Potomac River is near the center of the range of American eels and is a highly productive growth habitat compared with other USA estuaries (Fenske 2009). Harvest of yellow eels in the Potomac River region comprised 16% of the total USA harvest (by mass) on average during the past 57 years (A.C. Carpenter, Potomac River Fisheries Commission (PRFC), P.O. Box 9, Colonial Beach, VA 22443, USA, unpublished data). Results from the stock assessment were compared with the BRP to evaluate sustainability of the fishery.

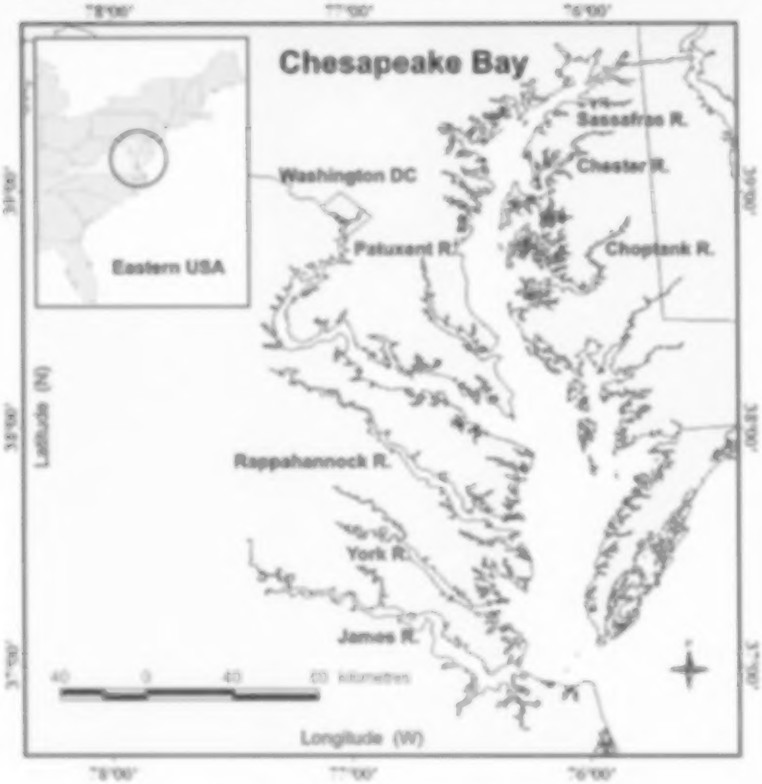
Materials and methods

Data

The ASSA model was fitted to an index of abundance based on commercial fishery catch per unit effort (CPUE, kg·pot^{-1}), a recruitment index based on a fishery-independent trawl survey, and proportional abundance-at-age data for 2007. A recruitment index was required for this model because a stock–recruitment relationship cannot be determined. Catch (kg) and fishery-dependent CPUE data were available from the PRFC during 1980–2008 and 1988–2008, respectively. Commercial harvests declined after peaking in the late 1970s and early 1980s (Fig. 2), similar to declining harvest across the entire North American range (MacGregor et al. 2009). Eel pots were the primary fishing gear accounting for >98% of reported catches during 1976–2008. Between 1988 and 2008, the number of active (i.e., those that reported catch) license-holding fishers declined from 50 to 15 (Fig. 2). Reported effort showed a corresponding decline from more than 142 000 reported eel pot lifts in 1988 to less than 49 000 in 2008.

Data on recruitment were available from the Virginia Institute of Marine Science (VIMS, Gloucester Point, Virginia) trawl survey, which used a stratified random survey in the lower Chesapeake Bay, collected between April and September in the York, James, and Rappahannock rivers, which are principal habitats (Tuckey and Fabrizio 2010; Fig. 1). The recruitment index was standardized using a general linear model that included year, river, depth, and a river by depth interaction and expressed as the log-transformed catch of 300–400 mm eels ($\log_e(\text{catch} + 0.01)$). Otolith-based aging indicated that 300–400 mm eels corresponded well to age-4 (Fenske 2009), but there was a broad range of ages potentially present within this size bracket. We chose age-4 as the recruitment age because age-4 was common in the fishery, but age-3 fish were very rare (Fenske 2009). Because length-at-age was highly variable, we also evaluated indices of

Fig. 1. Sub-estuaries of the Chesapeake Bay. Inset shows location in eastern USA.



recruitment from the VIMS survey for alternative size ranges: 200–400, 250–350, and 200–300 mm. These showed approximately the same trend as the one using 300–400 mm eels. Survey-caught eels are not regularly aged in the Chesapeake Bay region, leading to uncertainty regarding age structure of the recruitment index. Although no long-term fishery-independent survey exists for the Potomac River, the use of a recruitment index from other adjacent major Chesapeake Bay tributaries was reasonable based on their proximity to the Potomac River.

We sampled the commercial catch for proportional abundance-at-age in 2007. Otoliths from 168 females from the Potomac River eel pot fishery in 2007 were aged following the methods of Morrison and Secor (2003). Only relatively large females were present in the sample because it had been size graded, where the smallest eels were sold as bait prior to our inspection. Ages 7–11 were chosen for inclusion in the model because they were fully selected to the gear based on inspection of the catch curve, which resulted in a sample size of 60 individuals. Only 1 year of proportional abundance-at-age data was available because management agencies do not sample the catch for age or size composition in the Potomac River.

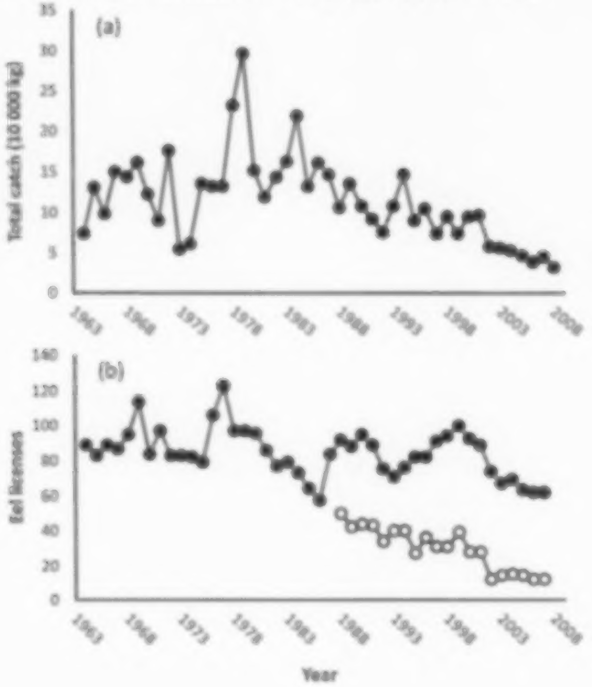
Stock assessment model

The ASSA model estimated abundance and exploitation rates and was sex-specific because American eels have sexually dimorphic growth and maturation. Females are larger and older at maturation and have higher growth rates (Tesch 1977; Helfman et al. 1987; Oliveira 1999). The model has underlying age-structured dynamics, assumes that total catch is known without error, and is fitted to an aggregate index of abundance. Catch reports for American eels in the Potomac River are thought to be quite accurate during the period included in the model (A.C. Carpenter, PRFC, Colonial Beach, VA 22443, USA, personal communication, 2010). The model included years 1980–2008 and ages 4 to 11+; the "plus" group served as an aggregate category for ages 11 and older. Some parameters were estimated outside the ASSA model, including natural mortality and age- and sex-specific maturation, selectivity, and mean individual mass. Because American eels are semelparous, they mature, leave their juvenile habitat, and spawn only once. Maturation mortality was included in the model to allow estimation of female spawner escapement. We approximated the 95% confidence intervals of model estimates as the maximum likelihood estimate (MLE) ± 2 times their asymptotic standard errors.

The process model described how abundance changed over time (see Table 1 for variable definitions). Recruitment (abundance at age-4) was estimated for each year and sex by the product of the sex ratio and overall recruitment for each year:

$$(1) \qquad R_{y,g} = T_y s_g$$

Fig. 2. (*a*) Total catch (in 10 000 kg) of American eels in the Potomac River, 1964–2008 (A.C. Carpenter, Potomac River Fishery Commission, P.O. Box 9, Colonial Beach, VA 22443, USA, unpublished data). (*b*) Number of licensed American eel pot fishers in the Potomac River (black circles, 1964–2008) and number of American eel pot licenses that reported catches (grey circles, 1988–2008).



We assumed a 1:1 sex ratio for age-4 eels. Recruitment was estimated as a free parameter for each year. We took this approach because local recruitment may not be tied to local spawning stock abundance. The model did not include any penalty on deviations for mean recruitment because recruitment had declined substantially in some regions, and we did not want to cause attenuation of the parameter estimates.

Abundance-at-age in1980 was calculated assuming the Potomac stock was in equilibrium. Abundance in the next age was equal to the product of abundance in the previous age, the exponential mortality model where fishing mortality-at-age and sex was based on fishery selectivity, and the proportion of individuals that did not mature:

$$(2) \qquad N_{1980,a+1,g} = N_{1980,a,g}\,\mathrm{e}^{-M}(1 - S_{a,g}U_{\mathrm{init}})(1 - m_{a,g})$$

Maturation mortality occurred after other natural mortality sources, and the equilibrium exploitation rate was estimated during model fitting. Abundance in the age-11+ group in 1980 was calculated using the solution to the infinite series for abundance for ages 11 and older:

$$(3) \qquad N_{1980,11+,g} = \frac{N_{1980,10,g}\,\mathrm{e}^{-M}(1 - S_{10,g}U_{\mathrm{init}})(1 - m_{10,g})}{1 - \mathrm{e}^{-M}(1 - S_{11+,g}U_{\mathrm{init}})(1 - m_{11+,g})}$$

For subsequent model years (1981–2008), abundance-at-age was calculated assuming the catch occurs instantaneously halfway through the year:

$$(4) \qquad N_{y+1,a+1,g} = (N_{y,a,g}\,\mathrm{e}^{-0.5M} - C_{y,a,g})\,\mathrm{e}^{-0.5M}(1 - m_{a,g})$$

Abundance of age-11+ eels was calculated as the sum of surviving age-10 and age-11+ eels from the previous year.

$$(5) \qquad \begin{aligned} N_{y+1,11+,g} = {} & (N_{y,11+,g}\,\mathrm{e}^{-0.5M} - C_{y,11+,g})\,\mathrm{e}^{-0.5M} \\ & \times (1 - m_{11+,g}) + (N_{y,10,g}\,\mathrm{e}^{-0.5M} - C_{y,10,g}) \\ & \times \mathrm{e}^{-0.5M}(1 - m_{10,g}) \end{aligned}$$

Because catch-at-age data were not available, catch-at-age (in numbers) for each sex was calculated from the product of total catch (in mass) and the proportional biomass of each age and sex class weighted by selectivity and converted from mass to numbers:

$$(6) \qquad C_{y,a,g} = \frac{X_y S_{a,g} N_{y,a,g}\,\mathrm{e}^{-0.5M}}{\sum_g \sum_a (S_{a,g}\,\overline{w}_{a,g} N_{y,a,g}\,\mathrm{e}^{-0.5M})}$$

Total biomass just prior to fishing was calculated as the product of abundance, mean mass, and survival during the first half of the year:

$$(7) \qquad B_y = \sum_g \sum_a N_{y,a,g}\overline{w}_{a,g}\,\mathrm{e}^{-0.5M}$$

Biomass of spawning females (SB) was calculated as the sum of maturing females over ages that survived and were not harvested:

$$(8) \qquad \mathrm{SB}_{y,g} = \sum_a (N_{y,a,g}\,\mathrm{e}^{-0.5M} - C_{y,a,g})\,\mathrm{e}^{-0.5M}\overline{w}_{a,g}m_{a,g}$$

Exploitable biomass was the biomass vulnerable to the fishery:

$$(9) \qquad \tilde{B}_y = \sum_g \sum_a N_{y,a,g} S_{a,g}\overline{w}_{a,g}\,\mathrm{e}^{-0.5M}$$

The annual exploitation rate for the Potomac stock was calculated as total observed annual catch divided by total biomass in that year:

$$(10) \qquad U_y = \frac{X_y}{B_y}$$

The observation model made predictions that were compared with the observations to estimate parameters. A recruitment index was estimated for each model year to compare with the standardized age-4 recruitment index:

$$(11) \qquad \hat{I}_y = T_y q_1$$

where the MLE of catchability was

$$(12) \qquad \log_e q_1 = \frac{1}{n_1}\sum_y (\log_e I_y - \log_e N_{y,4})$$

The estimated fishery CPUE index included density-dependent catchability:

Table 1. Parameters, data, and variables for Potomac River American eel assessment model.

Variable	Description
a	Age (i is also an age subscript in spawning potential ratio (SPR) calculations)
A	Plus group for maximum age (11) used in the model
y	Year
g	Sex
f	Female
B_y	Total biomass (kg) for year y
$\tilde{B}_y$	Exploitable biomass (kg) for year y
$C_{y,a,g}$	Catch (number of individuals) for year y, age a, and sex g
E_y	Fishery effort for year y (in 10 000 pot nights fished)
I_y	Recruitment index ($\log_e$ number of eels per tow) for year y
$m_{a,g}$	Proportion of eels of age a and sex g that will mature that year
M	Natural mortality rate (year^{-1})
n_e	Effective sample size for abundance-at-age data
n_1	Number of years of data for the first likelihood component
n_2	Number of years of data for the second likelihood component
$N_{y,a,g}$	Numbers-at-age a in year y for sex g
p	Proportional abundance-at-age for third likelihood component
q_1	Catchability for recruitment index
$q_{2,y}$	Catchability for fishery catch-per-unit-effort (CPUE) index
$R_{y,g}$	Estimated recruitment of American eels in year y for sex g
s_g	Sex ratio of age-4 American eels
$S_{a,g}$	Selectivity-at-age for eels age a and sex g
SB_y	Spawner biomass (female kg) for year y
SB/R_F	Spawner biomass per recruit for fished population
SB/R_U	Spawner biomass per recruit for unfished population
SPR	Spawning potential ratio
T_y	Total recruitment, sexes combined, in year y
U_{init}	Equilibrium exploitation rate prior to 1980
U_y	Exploitation rate in year y
$\bar{w}_{a,g}$	Mean mass-at-age (kg) for individual eels age a and sex g
X_y	Observed catch (kg) for year y
α, β	Parameters of effort-dependent catchability
σ_1	Standard deviation for recruitment index
σ_2	Standard deviation for fishery CPUE index
σ_{rw}	Standard deviation for catchability in the random walk model
σ_{wn}	Standard deviation for catchability in the white noise model

$$(13)\qquad \widehat{\mathrm{CPUE}}_y = \tilde{B}_y q_{2,y}$$

where fishery catchability was estimated for each year using a density-dependent catchability model (Paloheimo and Dickie 1964; Wilberg et al. 2010):

$$(14)\qquad q_{2,y} = \alpha \tilde{B}_y^{\beta}$$

Density-dependent catchability has been observed in fishery-dependent indices of abundance for many stocks and can be caused by nonrandom search by fishers on a contagiously distributed stock and by gear saturation (Wilberg et al. 2010). We used a density-dependent catchability model for fishery CPUE because it was very robust to changes in the standard deviation (SD) of the CPUE index.

Model fitting

The model was constructed in AD Model Builder (Otter Research Ltd., Sidney, British Columbia), and parameters were estimated using maximum likelihood estimation. The model was fitted by minimizing the negative log likelihood function (–LL), which contained components for the recruitment index (L_1), the fishery CPUE index (L_2), female proportional abundance-at-age in 2007 (L_3), and a penalty to constrain the equilibrium exploitation rate in the first year (L_4):

$$(15)\qquad -\mathrm{LL} = L_1 + L_2 + L_3 + L_4$$

The first likelihood component (L_1) compared the observed and predicted recruitment index for each year:

$$(16)\qquad L_1 = n_1 \log_e \sigma_1 + \frac{\sum \left[\log_e(I_y) - \log_e(q_1 \hat{N}_{y,a=4})\right]^2}{2\sigma_1^2}$$

We assumed that errors in the recruitment index were lognormally distributed with an SD (on the log scale) of 0.3. This value was slightly greater than the estimated standard error of the log-scale recruitment index (~0.2), but because the recruitment index was not specific to the Potomac River, we wanted to capture the potential for additional variation. Additionally, the estimated precision of the index of recruitment

(0.2) is a lower threshold for the relationship between the recruitment index and actual recruitment because it only includes variability in survey catch (Wilberg et al. 2010).

The second likelihood component (L_2) compared the observed and predicted fishery CPUE index:

$$(17)\quad L_2 = n_2 \log_e \sigma_2 + \frac{\sum \left[\log_e(\mathrm{CPUE}_y) - \log_e(\widehat{\mathrm{CPUE}}_y)\right]^2}{2\sigma_2^2}$$

We assumed errors in the fishery CPUE index were lognormally distributed with a log-scale SD of 0.3 and tested the sensitivity of the model to this assumption. We chose this SD so that the fishery CPUE index would have an equal weight to the recruitment index. An SD of 0.3 is somewhat higher than 0.15–0.2 recommended by Francis et al. (2003) for commercial fishery-dependent indices in New Zealand.

The third likelihood component (L_3) compared the observed and predicted proportional abundance-at-age for female ages 7–11 in 2007 using a multinomial likelihood function (Fournier and Archibald 1982):

$$(18)\quad L_3 = -n_e \sum_{a=7}^{11} p_a \log_e \hat{p}_a$$

Because effective sample size is typically lower than the number of individuals aged (Crone and Sampson 1998), we selected an effective sample size for proportional abundance-at-age that was half the number of American eels aged (n = 30).

A penalty on the equilibrium exploitation rate prior to the first year of the model was necessary to estimate the parameter. The number of days fished during 1976–1979 was 20% higher than in 1980. Thus, we included a lognormal penalty on the equilibrium (median) exploitation rate, which was 20% higher than the 1980 exploitation rate and a log-scale SD of 0.3:

$$(19)\quad L_4 = \frac{0.5\left[\log(u_{\mathrm{eq}}) - \log(1.2u_{1980})\right]^2}{0.09}$$

This was the highest level of coefficient of variation (CV) we could choose and still have the model converge.

Biological reference points (BRP)

In addition to the ASSA model, we developed a spawning potential ratio (SPR) model for female American eels to estimate an exploitation rate BRP and compared the estimated exploitation rates with the BRP. The SPR model predicted the equilibrium spawning biomass of females produced per female recruit:

$$(20)\quad \mathrm{SB}/R_F = \sum_{a=4}^{\infty} \left[e^{\sum_{i=4}^{a-1} -M} \bar{w}_{a,f} m_{a,f} \prod_{i=4}^{a-1} (1 - S_{i,f}u)(1 - m_{i,f}) \right]$$

Values for the parameters of the SPR model (natural mortality, maturation-at-age, selectivity-at-age, and mass-at-age) were identical to those for females in the ASSA model. SPR was calculated as the (female) spawning biomass per recruit of American eels in a fished population divided by the spawning stock biomass per recruit in an unfished population:

$$(21)\quad \mathrm{SPR} = \frac{\mathrm{SB}/R_F}{\mathrm{SB}/R_U}$$

The SB/R_U for an unfished population was calculated using eq. 20, but with the exploitation rate set equal to zero. We calculated $F_{50\%}$, the exploitation rate that results in a 50% reduction of the SPR (Quinn and Deriso 1999), and the estimated SPR for each year. $F_{50\%}$ has been suggested as a precautionary reference point for European eel (International Council for the Exploration of the Sea 2001).

Parameters estimated outside of the model

American eel are a relatively data-poor species, and published estimates of biological parameters such as selectivity, maturation, and natural mortality are rare or vary substantially by region. Additionally, the age- or size-structured data that are necessary to estimate these parameters during model fitting are not available for the Potomac River. Few estimates of natural mortality exist for American eels. Instantaneous natural mortality was assumed to be 0.24 year^{-1}, based on catch curve estimates from the unfished American eel stock in the Hudson River. To obtain this estimate, we conducted catch curve analysis based on Hudson River data from Morrison and Secor (2003), but catches-at-age were first rescaled by the observed decline in recruitment in the Chesapeake Bay and St. Lawrence River (Casselman et al. 1997). Estimated maturation mortality was subtracted from the catch curve mortality estimates to obtain the natural mortality estimate.

Female maturation-at-age is thought to be length-based (Vøllestad and Jonsson 1986; De Leo and Gatto 1996). We estimated maturation-at-age for females by fitting a logistic model to data from American eels collected throughout the Chesapeake Bay. Gonads of 345 females, aged 4–11, were collected in fall 2007 from the Chester, Choptank, James, and Potomac rivers and macroscopically inspected. A female exhibiting a gonado-somatic index (GSI) ≥1% may mature in the present year and subsequently undertake an oceanic spawning migration (Durif et al. 2005). We assumed females with a GSI ≥ 0.9% (19% of female sample) would mature that year. Female maturation-at-age never exceeds 20% in our estimation. This was similar to the finding of De Leo and Gatto (1996), who found that the percentage of European eel females maturing reached an asymptote at approximately 10%–30%·year^{-1} in the systems and years they considered. Our assumed upper level of maturation-at-age is consistent with the maximum observed age of 18 in Chesapeake Bay (Owens and Geer 2003).

Male maturation-at-age was estimated using data collected from eels sampled in the Chester, Choptank, James, Patuxent, Potomac, and Sassafras rivers in 2007. Gonad development of 185 male and intersexual eels aged 3–8 was examined macroscopically. Male European eels, and presumably American eels, develop directly from intersexual eels (Buellens et al. 1997). Males were identified on the basis of gonad morphology as described in Buellens et al. (1997) (i.e., gonads with individual, overlapping lobes). Male American eel are thought to use a "time minimization" strategy, where they mature and migrate at the earliest possible age (Oliveira 1999). Given this strategy, we assumed that any American eel that was identifiable as male would mature in the current year. We used the ratio of male to intersexual eels at each age to estimate the proportion mature, and maturation was constant over ages 4–7. Owing to the lack of male or intersexual American eels older than 8 years in the Chesapeake Bay samples, we assumed a maturation-at-age of 0.99 for males aged 8–11 (Fig. 3). This was a similar result to De Leo and Gatto (1996), who found that by age 4–7 years, all males had likely matured.

Mean individual mass-at-age for female and male American eels was calculated using the mass and age data collected from the Chester, Choptank, James, Patuxent, Potomac, and Sassafras rivers (Fenske 2009; Fig. 3). Because of a lack of older males in samples, we extrapolated mean mass-at-age for male and intersexual eels aged 9–11 using a linear mass-at-age regression from ages 3 to 8.

Because age-specific catch data were not available for the Potomac River, we estimated fishery selectivity outside of the model fitting. Eel pots with a 12.7 mm mesh are the primary gear used in the commercial fishery in the Potomac River. To calculate female selectivity-at-age, we fit a von Bertalanffy growth curve to female length-at-age data from Owens and Geer (2003; for ages 1–3) and length-at-age data from 2007 collected by Fenske et al. (2010) (for ages 4–11). Male length-at-age was modeled as a linear function using length-at-age data collected in 2007 (Fenske 2009). We then calculated the proportion of male and female American eels greater than 270 mm for each age in the model, assuming a normal distribution and the SDs of length-at-age from Owens and Geer (2003). The 270 mm threshold size was chosen as the midpoint between the minimum length (220 mm) commonly retained by eels pots with 12.7 mm mesh and a minimum length (320 mm) that should always be retained by the pots. These length thresholds were based on a length–girth relationship developed from measurements of 820 eels from the Chesapeake Bay in 2007 (Fenske 2009). Male eels were never fully selected in the model, which was reasonable because some may mature before reaching the size of full selection used in this model (Oliveira 1999).

Sensitivity analyses

We performed sensitivity analyses to examine the effects of our assumed natural mortality rate, the SDs for both indices of abundance, selectivity, and time-varying catchability model for fishery CPUE. For natural mortality and the SD of the fishery CPUE index, we increased and decreased the values by 20%–50% and compared these alternate model outputs with the base model (the ASSA model specified in the methods). In addition we tested the sensitivity of the model to two different selectivity patterns by choosing a larger (320 mm) and a smaller (220 mm) length threshold for calculating selectivity-at-age. These alternate length thresholds represented the length at which eels were fully selected to the gear and the length at which less than 0.1% were retained by the gear, respectively.

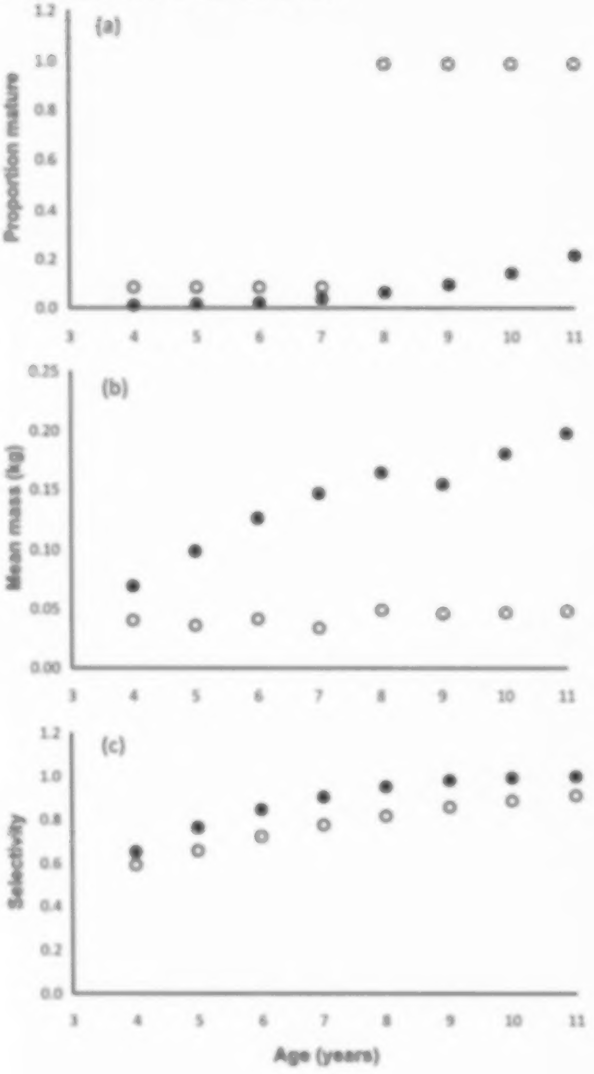
We conducted sensitivity analyses of four alternative models for fishery catchability: white noise, random walk, effort-dependent, and constant. Each catchability pattern was run with three values for the SD of the recruitment index (0.2, 0.3, 0.4). The white noise model (i.e., random variation about a constant mean on the log scale) was

$$q_{2,y} = \bar{q}_2 e^{\delta_y} \tag{22}$$

The white noise model also required an additional likelihood component for the annual deviations from mean catchability:

$$L_5 = \frac{1}{2\sigma_{wn}^2} \sum_{y=1988}^{2008} \delta_y^2 \tag{23}$$

Fig. 3. Mean maturity-at-age (*a*), mass-at-age (*b*), and selectivity-at-age (*c*) used in the age- and sex-structured assessment (ASSA) model for female (black circles) and male (grey circles) American eels. Data came from published literature and laboratory dissections of American eel in the Chesapeake Bay.



We used two values for the SD of the process errors, 0.25 and 1.0.

The random walk catchability model was

$$(24)\qquad q_{2,y+1} = q_{2,y}\, e^{\delta_y}$$

The random walk catchability model also required an additional likelihood component:

$$(25)\qquad L_5 = \frac{1}{2\sigma^2_{rw}} \sum_{y=1989}^{2008} \delta_y^2$$

We used two values for the SD of the process errors: 0.25 and 1.0. For the random walk catchability model, $q_{2,1988}$ is an estimated parameter.

The effort-dependent catchability model was

$$(26)\qquad q_{2,y} = \alpha E_y^{\beta}$$

where α and β were estimated parameters. The last catchability model assumed constant catchability for fishery CPUE.

For all sensitivity analyses, we compared the following with the base model values: the estimates of average total abundance during 1980–2008, total abundance in the first and last year of the model, average exploitation rate during 1980–2008, and exploitation rate in 2008.

Results

The ASSA model fit the observed fishery CPUE index, recruitment index, and proportion-at-age reasonably well, but a slight residual pattern was present in the fit to the fishery CPUE index (Fig. 4). Predicted fishery CPUE increased 11.9% during 1988–2008, in contrast with the recruitment index. Residuals for fishery CPUE showed a U-shaped pattern with positive residuals at the beginning and end of the time series and negative residuals in the middle. Observed and predicted recruitment indices decreased substantially during 1980–2008, and the model fit the observed index nearly perfectly when the recruitment index was the only source of data. Model predictions of the age composition in 2007 showed the same pattern of decreasing proportions with increasing age as the observed proportions-at-age (Fig. 4).

Estimated female spawner biomass declined to 6.4% of its 1980 value (Fig. 5). The estimates had a large CV early in the time series, but the uncertainty decreased with more data. The primary reason for the large amount of uncertainty in the first year was due to U_{init} (median 0.17; 95% confidence interval (CI) 0.04–0.68). Estimated abundance (in numbers) declined substantially to 7.8% of its 1980 value during 1980–2008 (Table 2). Estimated abundance was relatively high from 1980 to 1984 then began to steadily decline in 1985. The estimated abundance in the Potomac River in 2008 was less than 2.4 million American eels. Estimated recruitment in 2008 was 17.7% of the 1980 value (Table 2; MLE q_1: 5.72×10^{-9}, 95% CI: 4.60×10^{-9} to 6.85×10^{-9}). Estimated catchability in the fishery increased steadily during 2002–2008 as American eel biomass decreased (Fig. 5), and the parameters of the density-dependent catchability function had relatively narrow 95% CIs (MLE α: 7.42×10^{-6}, 95% CI: 6.00×10^{-6} to 9.17×10^{-6}; MLE β: −1.05, 95% CI: −1.22 to −0.88).

In contrast with abundance, estimated exploitation rate increased over time (Fig. 5). The exploitation rate that corresponded to the BRP $F_{50\%}$ was 0.14 year^{-1}. The exploitation rate for fully selected females was higher than the $F_{50\%}$ reference point since 1993. Between 1996 and 2008, the estimated exploitation rate was higher than $F_{30\%}$: 0.25 year^{-1}.

Sensitivity analysis

Most of the models with different catchability assumptions were very sensitive to the assumed SD of the recruitment index (Table 3). However, two notable exceptions were the density-dependent catchability model and the white noise model with a log-scale SD of 1.0. These two models were insensitive to assumed SD of the recruitment index, with a small (3%–13%) difference in range of estimated mean abundance across the range of assumed SD for the recruitment index. In comparison, the constant, effort-dependent, random walk, and white noise (with log-scale SD of 0.25) catchability models were more sensitive to assumed recruitment index SD, with a large range (43%–80%) of differences in estimated mean abundance across models. In several catchability scenarios, the model would not converge on a solution. Abundance in the first and last years showed a similar pattern to average abundance, and exploitation rate showed the opposite pattern.

The model was moderately sensitive to assumptions of natural mortality, the SDs of fishery CPUE and recruitment indices, and selectivity patterns, based on the percent difference of the base model and alternative model results (Table 4). A 25% increase in natural mortality caused estimated exploitation rates in 2008 to decrease by approximately 13% and abundance in 2008 to increase by 15% over the base model. A 17%–38% decrease in natural mortality caused estimated exploitation rates for females and males in 2008 to increase by approximately 9%–29% and 2008 abundance to decrease by 10%–24%. Increasing or decreasing the minimum size for the selectivity estimates by 19% caused changes of 13%–43% for 2008 abundance and 13%–30% for exploitation rate (Table 4). Increasing or decreasing the SD for the fishery CPUE index by 50% resulted in mean abundance and mean exploitation rates changing by <2% and <5%, respectively. Changing the SD for fishery CPUE also resulted in changes to how well the recruitment index was fitted, but the model was always matched the observed recruitment index very closely (median absolute value of percent deviation ≤ 0.2%).

Discussion

We detected a substantial decline in American eel abundance in the Potomac River between 1980 and 2008. The decline was of a similar magnitude and on the same time scale as the decline in abundance seen in other parts of the American eel's range and for European eel (Casselman et al. 1997; Committee on the Status of Endangered Wildlife in Canada 2006; International Council for the Exploration of the Sea 2006). Since the 1970s, the number of yellow-phase American eels ascending eel ladders at the Moses–Saunders Hydroelectric Dam at Cornwall, Ontario, has declined by about 99%. Between 1980 and 2008, the Chesapeake Bay recruitment index from the VIMS trawl survey has declined by 82%, and the 2006 Atlantic States Marine Fisheries Commis-

Fig. 4. Model fit for observed and estimated fishery catch per unit effort (CPUE) (*a*), recruitment CPUE (*b*), and female age composition in 2007 (*c*). Model estimates are represented by the solid lines and observed data by solid circles. The 95% confidence intervals for the predicted CPUE and age composition are indicated by dashed lines.

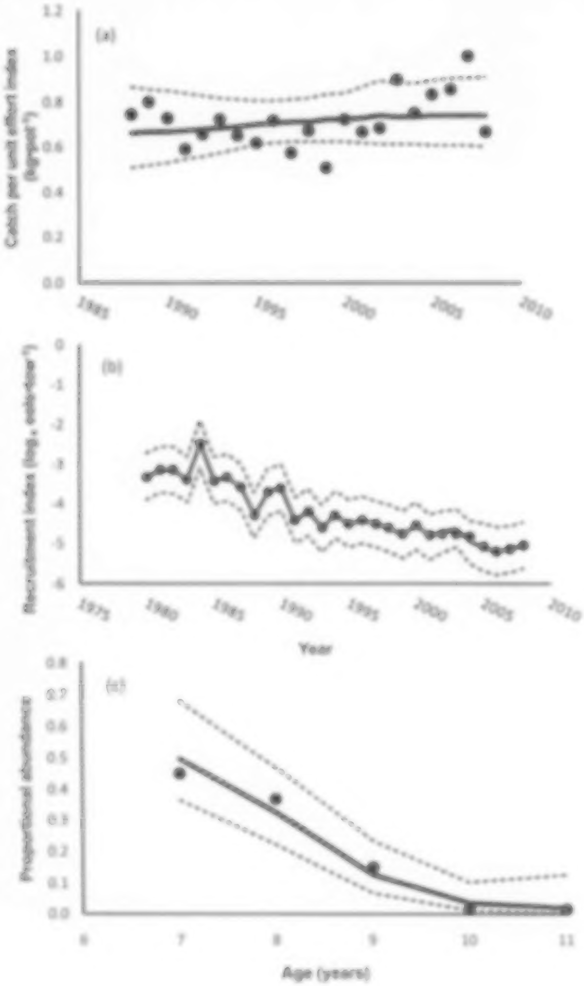
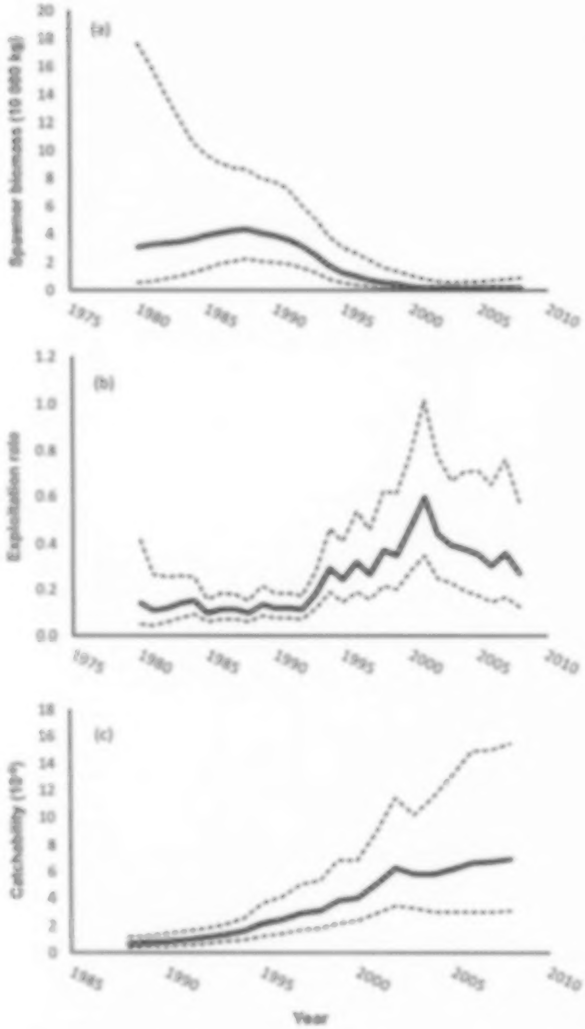


Fig. 5. (*a*) Estimated spawner biomass (10 000 kg) for female American eels from the Potomac River, 1980–2008. (*b*) Estimated exploitation rate for female American eels in the Potomac River, 1980–2008. (*c*) Model-estimated catchability of American eels in the Potomac River, 1988–2008. For all figures, the 95% confidence intervals for the predicted parameter are indicated by the dashed lines.



sion stock assessment for American eel also indicated that the stock was "at or near documented low levels" (Atlantic States Marine Fisheries Commission 2006). Similar declines in abundance and recruitment have been observed for European eel (Dekker 2000; International Council for the Exploration of the Sea 2006), a species that shares spawning grounds in the Sargasso Sea with American eel (McCleave 1993). The coincidence of declining recruitment and abundance in three distant regions of anguillid eels points to large-scale (population-wide) processes as an important component of anguillid population dynamics. The decline predicted by the model also serves as a diagnostic; the model results were consistent with observed declines in American eel recruitment in the Chesapeake Bay and elsewhere.

The abundance estimates from our ASSA model were heavily influenced by trends in the recruitment index from tributaries of the lower Chesapeake Bay, and the model fit the recruitment index nearly exactly (absolute value of the median deviation was 0.1%). We believe these abundance estimates reflect a true decline in abundance of yellow-phase American eels. Our model indicated that female spawner escapement from the Potomac River decreased by 94% between 1980 and 2008. For American eels, spawning stock biomass may have decreased to levels that impair recruitment, possibly due initially to overharvest (Atlantic States Marine Fisheries Commission 2000; de Lafontaine et al. 2010), habitat

Table 2. Age- and sex-structured assessment model estimates of American eel abundance-at-age (×10 000) during 1980–2008 in the Potomac River.

	Age								
Year	4	5	6	7	8	9	10	11+	Total
1980	641.0	429.6	282.2	182.0	115.1	39.1	22.9	26.3	1738.0
1981	760.6	432.6	284.6	183.7	116.2	39.5	23.2	26.6	1867.1
1982	760.4	527.4	295.8	191.9	121.9	41.7	24.6	28.2	1991.9
1983	593.6	521.8	356.3	196.7	125.5	43.2	25.5	29.3	1891.9
1984	1451.4	402.1	347.2	233.0	126.4	43.7	25.8	29.8	2659.4
1985	583.5	972.5	264.2	223.8	147.3	43.2	25.6	29.7	2289.9
1986	627.8	408.3	671.9	180.2	150.4	53.9	27.3	31.8	2151.5
1987	489.6	432.7	277.2	449.5	118.6	53.8	33.2	33.1	1887.7
1988	240.2	338.0	294.3	185.8	296.4	42.6	33.2	37.3	1467.8
1989	431.4	168.2	233.7	201.0	125.0	109.1	26.9	40.6	1336.0
1990	486.8	292.4	112.0	153.0	129.2	43.8	65.3	36.5	1319.0
1991	211.7	334.6	197.9	74.7	100.3	46.2	26.8	57.7	1049.9
1992	261.7	145.6	226.7	132.0	49.0	35.9	28.3	46.6	925.8
1993	174.7	181.0	99.3	152.3	87.3	17.7	22.2	41.9	776.4
1994	243.1	114.1	115.5	61.9	92.9	28.7	9.9	32.4	698.6
1995	194.1	144.7	65.2	63.5	32.9	25.8	13.6	17.8	557.6
1996	213.7	120.6	86.9	38.0	35.9	9.7	13.3	14.6	532.7
1997	193.3	124.4	67.1	46.4	19.5	9.3	4.4	11.5	476.0
1998	174.2	117.7	73.0	38.1	25.5	5.4	4.6	7.0	445.6
1999	147.4	96.9	61.9	36.6	18.2	6.0	2.3	4.4	373.6
2000	184.6	83.4	52.1	31.8	18.0	4.4	2.6	2.6	379.4
2001	140.0	92.8	38.8	22.6	12.9	3.4	1.5	1.6	313.5
2002	161.6	61.1	36.1	13.6	7.2	1.7	0.8	0.6	282.8
2003	172.9	83.8	29.5	16.4	5.8	1.3	0.6	0.5	310.9
2004	124.5	94.2	43.0	14.4	7.6	1.2	0.5	0.4	285.7
2005	108.0	68.9	49.3	21.4	6.9	1.6	0.5	0.3	256.9
2006	98.1	61.0	37.0	25.2	10.5	1.5	0.7	0.3	234.3
2007	103.3	57.8	34.4	20.1	13.2	2.6	0.7	0.4	232.7
2008	113.4	58.1	30.9	17.5	9.8	3.1	1.1	0.5	234.4
2009	—	69.0	34.1	17.5	9.6	2.6	1.5	0.7	—

Note: Recruitment in 2009 was not estimable, but abundance-at-age for the remaining ages is presented.

loss (Busch et al. 1998; Atlantic States Marine Fisheries Commission 2000), changing oceanic conditions, or increasing natural mortality. Mortality or curtailed spawning migrations due to impoundments, turbine mortality, or infection by the *Anguillicola crassus* parasite could be further depressing reproduction (McCleave 2001; Kirk 2003; Palstra et al. 2007). Changing oceanic conditions may have depressed marine primary production, leading to poor feeding conditions and reduced survival for eel leptocephali (Friedland et al. 2007; Bonhommeau et al. 2008).

A petition to list American eel as an endangered species in the USA was filed in 2004, but the US Fish and Wildlife Service (USFWS) found that the listing of American eel was not warranted (United States Fish and Wildlife Service 2007). A central rationale for USFWS not to list American eels as endangered centered on stable trends of glass eel (earliest juvenile stage) abundance indices (United States Fish and Wildlife Service 2007). Indeed, glass eel indices from New Jersey, North Carolina, and two in Nova Scotia, all beginning in the mid- to late 1980s, indicate no trend in recruitment over time (Sullivan et al. 2006; Committee on the Status of Endangered Wildlife in Canada 2006). For a long-lived species, a recruitment index of 15 years may be insufficient to capture population trends. These glass eel trends are counter to the observed changes in yellow eel abundance from Chesapeake Bay and other estuaries and demonstrate the difficulty in assessing American eel status based on a single life stage. If the glass eel indices are a true representation of eel population abundance, then declining yellow eel abundances would be attributable to decreasing survival between the glass eel and yellow eel phases. Although speculative, the decreased size of glass eels observed in New Jersey since the mid 1980s and decreased energetic status of European eel elvers (Edeline et al. 2006; Sullivan et al. 2006) could point to decreased survival between the glass eel and yellow eel phases. Alternatively, because glass eel abundance is highly variable from year to year, trends are difficult to detect, and recruitment indices based on yellow-phase eels may be more reliable. We used CPUE of 300–400 mm American eels in the VIMS trawl survey in Virginia tributaries of Chesapeake Bay as an index of age-4 recruitment in the Potomac River and examined indices based on three alternative size ranges. Use of a size-based index of abundance from a neighboring region presented two problems: (*i*) multiple ages comprised our index of abundance because of large overlaps in size at age for American eels (Owens and Geer 2003; Fenske et al. 2010), and (*ii*) the survey samples tributaries of Chesapeake Bay south of the Potomac River, which are under different

Table 3. Sensitivity analyses of recruitment variance for different catchability models within the age- and sex-structured assessment (ASSA) model.

	Adjusted						
Model	R_{var}	σ_{rw} or σ_{wn}	N_{1980}	$\bar{N}$	N_{2008}	$\bar{U}$	U_{2008}
Baseline DD	—	—	173.8	99.9	23.4	0.21	0.23
	0.2	—	176.5	101.5	24.0	0.21	0.22
	0.4	—	171.5	98.6	22.9	0.22	0.23
ED	0.2	—	244.1	149.2	44.9	0.11	0.10
	0.3	—	57.1	63.4	21.4	0.27	0.24
	0.4	—	50.8	50.6	18.6	0.35	0.29
CN	0.2	—	360.7	219.2	81.6	0.07	0.05
	0.3	—	49.6	44.7	23.9	0.40	0.21
	0.4	—	NC				
RW	0.2	0.25	356.0	214.8	74.8	0.07	0.06
	0.3	0.25	53.7	54.6	26.7	0.32	0.18
	0.4	0.25	NC				
	0.2	1.00	193.4	116.4	33.3	0.16	0.14
	0.3	1.00	159.4	101.7	32.2	0.17	0.15
	0.4	1.00	54.8	66.0	26.3	0.27	0.19
WN	0.2	0.25	335.2	200.9	69.1	0.08	0.06
	0.3	0.25	55.4	58.1	27.7	0.30	0.17
	0.4	0.25	NC				
	0.2	1.00	187.3	109.3	29.2	0.18	0.17
	0.3	1.00	174.1	102.8	29.4	0.19	0.17
	0.4	1.00	156.2	94.6	29.4	0.20	0.17

Note: The ASSA model assumed density-dependent (DD, baseline model) catchability with recruitment variance (R_{var}) of 0.3, but effort-dependent (ED), constant (CN), random walk (RW), and white noise (WN) catchability were also run. The first row represents the baseline model estimates for abundance in 1980 (N_{1980}, 100 000 eels); average abundance over years, ages, and sexes ($\bar{N}$, 100 000 eels); abundance in 2008 (N_{2008}, 100 000 eels); mean exploitation rate across year, ages, and sexes ($\bar{U}$); and average exploitation rate for 2008 (U_{2008}). Subsequent rows identify the adjusted recruitment variance value and indicate the model responses with respect to the baseline estimate. Models that did not converge are indicated by NC in the table.

Table 4. The model estimates from sensitivity analyses of alternative natural mortality rates (M), selectivity patterns, and standard deviation estimates for the fishery (SD_F) CPUE index used in the ASSA model for yellow-phase American eels in the Potomac River.

	Baseline	Adjusted	N_{1980}	$\bar{N}$	N_{2008}	$\bar{U}$	U_{2008}	% Dev
Baseline	—	—	173.8	99.9	23.4	0.21	0.23	0.1
M	0.24	0.15	148.0	88.3	17.7	0.23	0.29	0.1
		0.2	162.8	94.9	21.0	0.22	0.25	0.1
		0.3	190.2	107.7	26.9	0.21	0.20	0.1
Selectivity	270	220	160.4	91.5	20.4	0.24	0.26	0.1
		320	226.0	131.8	33.5	0.16	0.16	0.1
SD_F	0.3	0.2	172.8	99.5	23.1	0.22	0.23	0.2
		0.4	174.1	100.0	23.6	0.21	0.22	<0.1

Note: The first row represents the baseline model estimates for abundance in 1980 (N_{1980}, 100 000 eels); average abundance over years, ages, and sexes ($\bar{N}$, 100 000 eels); abundance in 2008 (N_{2008}, 100 000 eels); mean exploitation rate across year, ages, and sexes ($\bar{U}$); average exploitation rate for 2008 (U_{2008}); and median absolute value of the percent deviation between observed and predicted values for the recruitment index (% Dev). Subsequent rows identify the adjusted parameter value and indicate the difference in model response with respect to the baseline estimate.

regulations and potentially have different fishing mortality than the Potomac River so that the age composition may be different even if recruitment is the same. We thought it was reasonable to assume that the index represented age-4 American eels because they should be the dominant age class in the 300–400 mm range. To test the sensitivity of the model to an alternative model formulation that treated the index as a multiple-age index, we conducted two sensitivity analyses that assumed selectivity patterns for the VIMS trawl survey index. We conducted one run that assumed the selectivity of the "recruitment index" was equal for all ages across sexes and another run where we assumed that selectivity was equal for ages 4–6, but was zero for older ages. The results of these sensitivity analyses were similar to the base model. Estimated average abundance was 36% lower for the model with equal selectivity across all ages and 24% lower for the model with equal selectivity for ages 4–6. Abundance in the last year was much less sensitive to selectivity assumptions for the recruitment index, and both sensitivity runs were within 10% of the base model. We strongly recommend enhanced sampling and aging of American eels to increase certainty in recruitment indices.

Fishing mortality was an important component affecting the stock dynamics of American eels in the Potomac River, and current exploitation rates are too high if the goal is to match local anthropogenic effects with local productivity. The exploitation rates estimated by the ASSA model were much greater than $F_{50\%}$ for the past 16 years and greater than $F_{30\%}$ for the past 13 years. Additionally, estimated exploitation rates since 1996 were 12%–149% greater than the natural mortality rate (0.24 year^{-1}), which has been suggested as an upper threshold for sustainable fishing (Williams and Shertzer 2003). The total mortality rates estimated in the base model (natural mortality, maturation, and exploitation combined) were similar to total mortality estimates in the Chesapeake Bay (46%–76%·year^{-1}; Weeder and Hammond 2009) and indicate high mortality for American eel in the Chesapeake Bay region. Several sustainable levels of anthropogenic mortality for anguillid eels have been suggested. $F_{40\%}$ was recently adopted by the European Union for managing European eel stocks (Council Regulation (EC) 2007). $F_{50\%}$ has been suggested as a precautionary reference point for European eel (International Council for the Exploration of the Sea 2001), and given the observed decline in American eel and the difficulty in managing a data-poor, semelparous, and panmictic species, we suggest that a conservative reference point of $F_{50\%}$ is warranted for American eel.

Few comparable assessment models have been developed for American or European eels (e.g., De Leo and Gatto 1995), in part because of a lack of data. American eel landings are not routinely sampled for age or length composition (Atlantic States Marine Fisheries Commission 2006). Indices of abundance are only available in some parts of their range, and sex ratio, growth, and maturation can vary substantially among regions. Because of the data-poor situation of American eel fisheries, we made several assumptions about the selectivity, effective sample sizes, and SDs. In particular, we estimated selectivity outside of the model fitting, and estimated abundance was sensitive to changes in fishery selectivity. We believe we bracketed the range of potential gear selectivity patterns in our sensitivity analyses. However, fishing practices, such as decisions about where and when to fish, can also affect selectivity by targeting areas with the desired size of fish. We also specified the maturation schedule. Ideally, information on the age or size distribution of outmigrating silver eels would be used to estimate maturation at age (e.g., De Leo and Gatto 1995). Data on silver eels were not available for the Potomac River and are not routinely collected throughout most of the American eel's range. Finally, the model can easily be modified to include additional mortality sources, such as effects of turbine mortality on outmigrating silver eels, which are an important source of mortality in regions outside the Potomac River (McCleave 2001; Verreault and Dumont 2003). To model a system in which female spawner escapement was reduced by turbine mortality, eqs. 8 and 20 would be modified by multiplying SB or SB/R by $1 - \rho\tau$, where ρ is the proportion of the stock that must pass through turbines during outmigration and τ is the mortality rate from passing through a turbine. For the purpose of estimating SB/R under conditions of no additional anthropogenic mortality, ρ or τ should be set to zero.

The recruitment index and fishery CPUE index had conflicting trends that had to be reconciled within the model. This conflict among indices of abundance resulted in large differences among estimates for models with different assumptions about fishery catchability and observation error variance. Estimates from statistical catch-at-age models with different catchability assumptions have been shown to be highly sensitive to time-varying catchability (Wilberg and Bence 2006), so our results were not surprising. However, the density-dependent catchability model had remarkably consistent estimates of abundance and fishing mortality when different levels of observation error were assumed. Fishery CPUE data had little effect on estimated recruitment, perhaps implying that fishery CPUE was more informative about changes in catchability than population abundance. Density-dependent catchability has been observed in a substantial number of other fisheries (Wilberg et al. 2010) and is expected when fishers are able to target aggregations of fish (Paloheimo and Dickie 1964; Ellis and Wang 2007). Therefore, we used insensitivity of the model to observation error variance and the theoretical basis for density-dependent catchability as justification for selecting the density-dependent catchability model over the others. Continued development of methods for selecting among competing assessment models (e.g., Wilberg and Bence 2008) is necessary to develop robust model selection methods when candidate models differ in how they model random effects (e.g., deviations in catchability over time).

Declining American eel abundance and recruitment have raised concerns regarding the viability of the species under current management (Atlantic States Marine Fisheries Commission 2000). Because of variations in growth, maturation, sex ratios, and density of American eels throughout their range and a lack of population-wide abundance and recruitment indices, it is not feasible to develop a whole population model at this time. Although humans have little control over the oceanic phase of American eel life history, the status of the stock can be assessed relative to fishing in other regions, and fishing mortality (or other anthropogenic sources) can be reduced to meet target reference points and to promote adequate spawner escapement. However, a comprehensive, range-wide management plan for American eel is necessary to achieve sustainability because relative contributions to the spawning stock from different regions are unknown. One potential range-wide management plan is to assess and manage all regions of the range for locally sustainable anthropogenic mortality (e.g., harvest and turbine mortality). Managing all portions of a metapopulation sustainably is a robust management strategy under uncertainty about spatial dynamics (Tuck and Possingham 2000; Wilberg et al. 2008). While regional assessment and management has not been specifically evaluated for American eels, the approach could protect the population in each portion of its range and allow individuals from all areas to contribute to the spawning stock. The ASSA model proposed here could be applied in other regions, to the whole population if data became available, or to other anguillid eel stocks. This model could be a first step towards assessing American eel and reducing exploitation in regions where spawner escapement is too low.

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Water quality changes in south-central Ontario lakes and the role of local factors in regulating lake response to regional stressors

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Abstract: The long-term monitoring of eight lakes near Dorset, Ontario, indicates that the water quality has changed significantly over the last 30 years. However, trends in the Dorset lakes may not be representative of changes in other south-central Ontario lakes, as the Dorset lakes are within a small area and span a limited gradient of lake and watershed characteristics. To determine the regional extent of water quality changes, we assessed the chemical changes in 36 diverse lakes that were first sampled between 1981 and 1990 and were resampled in 2004–2005. Similar to trends in the Dorset lakes, changes in the regional lakes included decreasing acidity, calcium, conductivity, metals, and phosphorus, and increasing dissolved organic carbon, nitrogen, sodium, and chloride. Water quality changes were driven by regional stressors, including acidic deposition, climate, and lakeshore residential development. However, stressor-induced responses differed among lakes. Increases in sodium and chloride were greater in developed lakes that were close to winter-maintained roads. Site-specific characteristics, such as lake and watershed morphometry, could not explain heterogeneous changes in the remaining water quality parameters. These results indicate that other factors play an important role in regulating individual lake response to regional stressors.

Résumé : La surveillance à long terme de huit lacs près de Dorset, Ontario, Canada, révèle que la qualité de l'eau a changé significativement au cours des 30 dernières années. Cependant, les tendances observées dans les lacs de Dorset peuvent ne pas être représentatives du changement dans d'autres lacs du centre-sud de l'Ontario, parce que les lacs de Dorset se situent dans une région restreinte et couvrent un gradient limité de caractéristiques de lacs et de bassins versants. Afin de déterminer l'étendue régionale des changements dans la qualité de l'eau, nous avons évalué les changements chimiques dans 36 lacs diversifiés, échantillonnés d'abord entre 1981 et 1990, puis de nouveau en 2004–2005. Comme dans les tendances observées dans les lacs de Dorset, le changement dans les lacs de la région incluent une diminution de l'acidité, du calcium, de la conductivité, des métaux et du phosphore et une augmentation du carbone organique dissous, de l'azote, du sodium et du chlorure. Les changements dans la qualité de l'eau s'expliquent par les facteurs de stress régionaux, en particulier les précipitations acides, le climat et le développement résidentiel en bordure des lacs. Cependant, les réactions aux facteurs de stress ne sont pas les mêmes dans tous les lacs. L'augmentation du sodium et du chlorure est plus importante dans les lacs développés situés près de routes entretenues en hiver. Les caractéristiques spécifiques aux sites, telles que la morphométrie du lac et du bassin versant, ne peuvent pas expliquer les changements hétérogènes dans les autres variables de la qualité de l'eau. Nos résultats indiquent que d'autres facteurs jouent un rôle important dans le contrôle des réactions des lacs individuels aux facteurs de stress régionaux.

[Traduit par la Rédaction]

Introduction

Among Canada's most abundant natural resources are its over 3 million lakes covering 7.6% of the country's surface area (Environment Canada 2007). The ecological, financial, aesthetic, and public health ramifications of human-induced degradation of lakes are a predominant concern for Canadians, particularly in regions like cottage country in south-central Ontario where water-related activities are a central source of revenue (District Municipality of Muskoka 2005; Dillon et al. 2007). Lakes in this region have been subject to a number of anthropogenic stressors over the last few decades, including changes in acidic deposition, climate, and

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Table 1. Summary of stressors impacting the water quality of lakes near Dorset, Ontario.

Stressor	Response variable	Response	Mechanism	Reference
Sulphur deposition	Sulphate	↓	Decreased sulphur deposition	Dillon et al. 2003
	Alkalinity and pH	↑	Decreased sulphur deposition	Dillon et al. 2007
	Calcium, potassium, and magnesium	↓	Acidic leaching of soil reserves	Watmough and Dillon 2004
	Dissolved organic carbon	↑	Decreased acidity reduces photochemical loss and precipitation with metals	Keller et al. 2008
Climate warming	Sulphate	↑	Release of reoxidized sulphur from catchments following drought	Eimers et al. 2003
	Dissolved organic carbon	↑	Greater decomposition and release from soils under warm conditions	Keller et al. 2008
	Phosphorus	↓	Reduced export from catchments	Dillon and Molot 2005
Shoreline development	Sodium and chloride	↑	Winter road salting	Molot and Dillon 2008
	Calcium, potassium, and magnesium	↓	Forest growth after harvesting	Watmough and Dillon 2003
	Phosphorus	↓	Reduced loading following reforestation	Hall and Smol 1996

Note: The variables impacted by the stressors, the direction of response, and the mechanism causing the response are shown.

shoreline residential development. An examination of three decades of monitoring data for eight small (<100 ha) softwater (mean conductivity ranged from 20 to 36 $\mu S \cdot cm^{-1}$) lakes near Dorset, Ontario, indicates that these stressors have changed lake water quality (Table 1).

Lake water quality trends in the Dorset lakes suggest that there are significant stressor-induced impacts at a local scale. However, as human populations expand, anthropogenic impacts on inland lakes have increasingly become a regional concern. Although the primary stressors affecting change in the Dorset lakes operate on a regional scale, chemical change differs among lakes (Dillon et al. 2007; Keller et al. 2008; Molot and Dillon 2008), raising concerns about the regional applicability of the trends. This is actually a common problem. For example, inconsistent lake responses to changing acidic deposition levels have frequently been reported for eastern Canada, the northeastern USA, and Europe (Stoddard et al. 1998; Pilgrim et al. 2003; Skjelkvåle et al. 2005). Inconsistent responses to climate change and nutrient loading among neighbouring lakes have also been detected (Gunn et al. 2001; Søndergaard et al. 2005).

Inconsistent responses suggest that additional factors are regulating lake responses to regional stressors. For example, the time period that is considered can influence the detection of a lake's response to acidic deposition (Clair et al. 2002; Pilgrim et al. 2003) and likely influences the detection of a lake's response to other regional stressors. However, even when lakes are sampled over similar time periods, chemical changes can differ among lakes. Site-specific factors clearly influence lake water chemistry (Håkanson 2005) and may regulate chemical changes in lakes on the southern Canadian Shield (Quinlan et al. 2003; Eimers et al. 2008). Magnuson et al. (1997) recognized the importance of local factors and called for a predictive understanding of heterogeneous lake response to stressors. Blenckner (2005), expanding upon Magnuson et al. (2004), proposed a conceptual model incorporating a landscape filter (geographic position, watershed characteristics, and lake morphometry) and an internal lake filter (lake history and abiotic and biotic interactions) for predicting individual lake responses to climate change. It seems likely that these filters would also regulate lake responses to other stressors. There is some support for this hypothesis because lake and watershed characteristics, such as size, hydrology, and lake order, regulate stressor-driven changes in water chemistry (Arnott et al. 2003; Quinlan et al. 2003).

If site-specific factors regulate temporal change, regional predictions based on trends in the Dorset lakes may have limited generality because these lakes cover a small range of lake and watershed characteristics (Table 2). To determine the regional extent of lake water chemical changes in south-central Ontario, we examined 36 lakes spanning a gradient in lake and watershed characteristics. The specific objectives of this study were (*i*) to quantify regional-scale chemical changes in south-central Ontario lakes over a period of ~25 years, (*ii*) to determine whether the eight Dorset lakes reflect regional shifts in lake water chemistry, and (*iii*) to assess the importance of local factors (i.e., lake and watershed descriptors) in regulating a lake's chemical response to regional stressors.

Materials and methods

Study lakes

The eight Dorset lakes are within a 47 km radius in the Muskoka–Haliburton region of south-central Ontario (Fig. 1). These lakes have low productivity, low to moderate organic carbon content, and range from slightly acidic to neutral (Table 2). Seven of the Dorset lakes are headwater lakes. The 36 regional study lakes are within a 108 km radius and are located in the Muskoka and Parry Sound districts and Haliburton and Nipissing counties (Fig. 1). The regional lakes represent a much greater range in lake and watershed characteristics and water quality than the Dorset lakes (Table 2). The study region, which encompasses both sets of

Table 2. Summary of lake and watershed characteristics and water quality for the south-central Ontario study lakes.

		Dorset lakes ($n = 8$)			Regional lakes ($n = 36$)		
Descriptor	Abbreviation	Median	Minimum	Maximum	Median	Minimum	Maximum
Lake descriptor							
Area (ha)	A_0	54.5	21.4	93.6	96.7	2.3	679.0
Volume ($10^5 \cdot m^3$)	V	45.7	7.1	95.1	63.6	0.7	1099.0
Maximum depth (m)	Z_{max}	24.0	5.8	38.0	21.3	7.0	61.0
Elevation (meters above sea level)	ELEV	344.5	327.0	379.0	370.5	227.0	510.5
Shoreline length (km)	SHOREL	4.5	2.7	8.2	6.6	0.6	29.3
Development of shoreline[a]	D_L	1.7	1.6	2.4	2.0	1.2	3.7
Development of volume[b]	D_V	1.1	0.9	1.7	1.1	0.5	1.8
Runoff ($m \cdot year^{-1}$)	Q	0.51	0.47	0.55	0.49	0.39	0.58
Water residence time (years)	WRT	2.4	1.4	5.6	2.1	0.2	11.5
Distance to road (km)	ROADDIST	2.2	0.4	3.7	2.5	0.1	20.9
Shoreline building density[c]	DI	1.3	0.0	4.4	0.8	0.0	5.8
Watershed descriptor[d]							
Area[e] (ha)	A_W	339.1	71.7	532.4	396.4	32.5	10405.0
Perimeter (km)	PERIM	12.6	6.0	17.7	17.4	2.5	124.4
Main channel length (km)	$LENGTH_C$	2.8	1.1	4.3	4.3	0.1	21.7
Main channel slope ($m \cdot km^{-1}$)	$SLOPE_C$	7.8	2.1	10.5	5.3	0.0	43.9
Basin relief	RELIEF	44.1	17.4	95.2	67.7	25.4	186.9
Water quality variable							
Aluminum ($\mu g \cdot L^{-1}$)	Al	35.1	5.2	105.6	30.6	7.5	149.6
Alkalinity ($\mu equiv. \cdot L^{-1}$)	Alkalinity	33.1	9.5	97.4	43.3	−12.9	1180.7
Calcium ($\mu equiv. \cdot L^{-1}$)	Ca^{2+}	102.3	68.2	160.8	106.2	15.7	1179.0
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	Chl *a*	1.5	1.2	3.7	2.3	0.9	9.2
Chloride ($\mu equiv. \cdot L^{-1}$)	Cl^-	11.3	9.8	162.6	10.9	5.4	170.4
Colour (true colour unit)	Colour	—	—	—	14.0	2.8	148.9
Conductivity ($\mu S \cdot cm^{-1}$)	Conductivity	23.2	16.8	39.6	23.1	8.2	171.8
Dissolved inorganic carbon ($mg \cdot L^{-1}$)	DIC	1.0	0.4	1.4	0.9	0.2	14.3
Dissolved organic carbon ($mg \cdot L^{-1}$)	DOC	3.9	2.3	5.5	4.0	1.6	12.7
Iron ($\mu g \cdot L^{-1}$)	Fe	82.3	43.6	342.2	76.8	7.4	153.9
Potassium ($\mu equiv. \cdot L^{-1}$)	K^+	9.3	4.6	12.7	9.7	6.4	40.1
Magnesium ($\mu equiv. \cdot L^{-1}$)	Mg^{2+}	50.2	30.2	69.2	45.6	8.1	585.5
Manganese ($\mu g \cdot L^{-1}$)	Mn^{2+}	34.5	9.5	93.9	33.4	12.2	76.0
Sodium ($\mu equiv. \cdot L^{-1}$)	Na^+	33.0	22.0	111.7	32.0	4.2	183.1
Ammonia + ammonium ($\mu g \cdot L^{-1}$)	$NH_3 + NH_4^+$	21.7	13.5	26.9	21.1	9.2	59.2
Nitrate + nitrite ($\mu g \cdot L^{-1}$)	$NO_2^- + NO_3^-$	46.1	15.0	95.4	43.3	9.1	120.7
pH	pH	6.0	5.7	6.7	6.2	4.9	8.0
Reactive silicate ($\mu equiv. \cdot L^{-1}$)	SiO_3^{2-}	25.2	7.7	95.8	21.4	3.8	63.2
Sulphate ($\mu equiv. \cdot L^{-1}$)	SO_4^{2-}	105.4	96.2	128.8	104.1	25.0	565.1
Total inorganic nitrogen ($\mu g \cdot L^{-1}$)	TIN	67.7	31.0	108.9	70.4	23.7	154.7
Total Kjeldahl nitrogen ($\mu g \cdot L^{-1}$)	TKN	213.0	149.0	262.0	237.3	152.3	557.1
Total nitrogen ($\mu g \cdot L^{-1}$)	TN	291.9	164.0	301.7	292.3	182.1	566.2
Total organic nitrogen ($\mu g \cdot L^{-1}$)	TON	193.4	131.9	236.1	216.7	119.3	497.9
Total phosphorus ($\mu g \cdot L^{-1}$)	TP	6.5	4.7	10.5	6.5	3.1	27.8

Note: Water quality values are based on ice-free-season means for the year 2004 or 2005.

[a] Ratio of SHOREL to the circumference of a circle with area equal to A_0.

[b] Ratio of V to a cone of basal area equal to A_0 and height equal to Z_{max}.

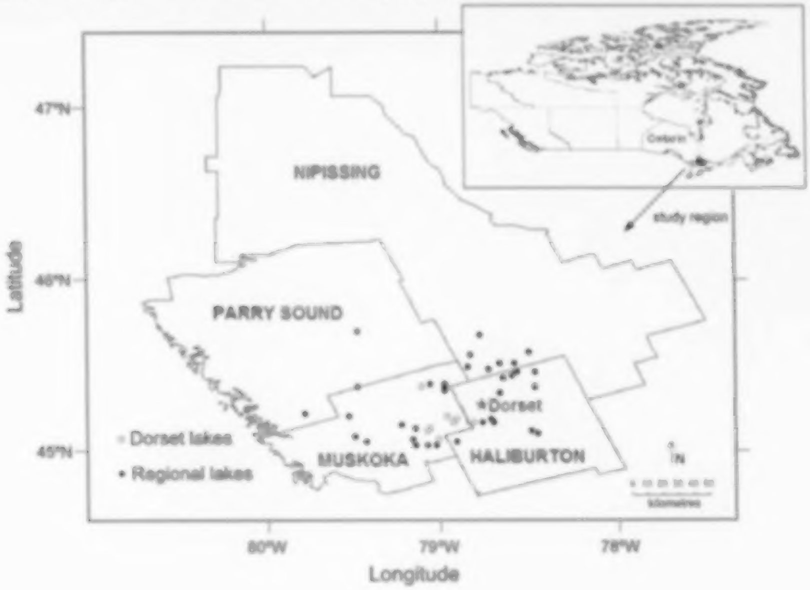
[c] No. of buildings$^{0.5} \cdot (A_0 \cdot Z_{max})^{-1}$.

[d] Owing to missing data, watershed descriptors for the regional lake set are based on 35 lakes.

[e] Does not include the study lake.

lakes, is within the boreal ecozone with a north temperate climate. From 1981 to 2005, the mean annual air temperature and total precipitation at the Muskoka airport weather station ranged from 4.0 °C to 7.3 °C and 777 to 1486 mm, respectively (Environment Canada 2008). The study region is on the Precambrian Shield and is primarily granitic bedrock overlain by thin (<1 m) glacial till and soil, although sporadic deeper deposits do occur. Riparian wetlands, swamps, and beaver ponds are common throughout the area. The study lakes are primarily within forested watersheds (secondary growth of mixed coniferous and deciduous trees) and have zero to moderate lakeshore development (seasonal and permanent residential homes and resorts). Lake access is by road or portage (<1.5 km), except for lakes in remote areas

Fig. 1. Location of the 8 Dorset long-term-monitoring lakes (indicated by open circles) and 36 south-central Ontario regional study lakes (indicated by solid circles). The inset shows the location of the study region (indicated by darkened area) within the province of Ontario.



of Algonquin Provincial Park where floatplanes allow access. The eight Dorset lakes were used to calibrate Ontario's Lakeshore Capacity Model, and 28 of the regional lakes were originally sampled to evaluate its applicability to other lakes in the region (Dillon and Rigler 1975; Hutchinson et al. 1991; Dillon et al. 1994). The eight additional regional lakes were later added to increase the range of acid sensitivity and dystrophy in the lake set. Many of the less-acidic lakes in the dataset have been used to characterize minimally impacted lakes as a reference to evaluate changes in other Precambrian Shield lakes (Holt and Yan 2003; Yan et al. 2004).

Sampling procedure and chemical analysis

The Dorset lakes were sampled each year from 1981 to 2005. The regional lakes were sampled for 1 year between 1981 and 1990 and then resampled in 2004 or 2005 following an identical field protocol. For a given year, sampling occurred monthly over the ice-free season (May–October) at a single station situated above the deepest point of each lake. Volume-weighted water samples (whole-lake samples during overturn periods and separate epi-, meta-, and hypolimnetic samples during thermal stratification) for chemical analyses were collected at the midpoint of every 2 m stratum using a peristaltic pump fitted with a polyvinyl chloride hose and were filtered through 80 μm mesh (Ingram et al. 2006; Girard et al. 2007). Unfiltered samples for chlorophyll *a* (Chl *a*, micrograms per litre) analysis were collected from the euphotic zone (estimated as double the Secchi disc depth). Analyses were performed at Ontario Ministry of the Environment labs in Dorset or Toronto following standard protocols and were subject to quality assurance procedures (Ontario Ministry of the Environment 1983; Locke 1990). For sampling dates during thermal stratification, epi-, meta-, and hypolimnetic samples were analyzed separately. The resultant values were weighted by the relative proportion of the water column that each stratum represented and summed to create monthly values. Ice-free-season means for Chl *a* and 23 chemical variables were then calculated from monthly May–October values. However, the average number of monthly samples available for the regional study lakes was 5.1 and 5.4 for the first and second sampling periods, respectively (means did not differ between sampling periods, 2-tailed *t*-test $p = 0.2$). This was largely due to lake inaccessibility in May. As the inclusion of May values did not influence ice-free-season means or our results (paired *t*-test *p*-values ≥ 0.05), we chose to include available May values.

Lake and watershed descriptors

We selected lake and watershed descriptors (Table 2) available from Girard et al. (2007) and the Ontario Flow Assessment Techniques version 1.0 database maintained by the Ontario Ministry of Natural Resources (Chang et al. 2002). In addition, lake runoff estimates were obtained from Canada Department of Fisheries and Environment (1978) values that were updated and collated into a look-up table. These values were interpolated at a spatial grid size of 1 min × 1 min. Topographical maps (Natural Resources Canada 2006) were used to measure the shortest linear distance between a lake's perimeter and the nearest county-maintained road. The number of buildings within 100 m of a lake's shoreline was enumerated from geographical information systems maintained by government agencies (County of Haliburton 2005; Natural Resources Canada 2006) or obtained from cottage associations. The number of buildings was then square root transformed and divided by lake area multiplied by maximum lake depth as a comparative index of volume-weighted lakeshore development (e.g., Wilkinson and Smol 1998).

Statistical analysis

Temporal changes in water quality

Changes in lake water quality were assessed using SAS version 9.1.3 (SAS Institute Inc. 2003). As water quality variables were paired (i.e., ice-free-season means were calculated for two sampling periods per lake), their differences were examined for normality (Zar 1999). Where necessary, variables were log transformed to ensure that normality requirements of parametric analysis were met. Eight regional lakes were not analyzed for colour during the first sampling period, so ice-free-season colour was estimated using a linear relationship based on colour in the 28 other lakes: log(colour) = 1.778·log(dissolved organic carbon) + 0.286; $R^2 = 0.90$, $p < 0.001$. Colour was not available for the Dorset lakes.

Overall temporal change in water quality for the regional lake set was assessed by doubly-multivariate repeated measures analysis (generalized linear model procedure for SAS), which detects differences over time for multiple response variables (i.e., chemistry) that are measured across multiple subjects (i.e., lakes) (Tabachnick and Fidell 1996). Paired sample *t*-tests were then used to identify the direction of significant temporal change in individual variables. Because of increased risk of type-I error due to multiple comparisons, we also calculated the false discovery rate (FDR) for the paired sample *t*-tests (Benjamini and Hochberg 1995; García 2004). As the time interval between sampling events for the regional lakes ranged from 14 to 24 years (Table 3), the rate of change in water quality values is reported. These rates were calculated by dividing the difference in water quality between the second and first sampling periods by the number of years between sampling events.

The rate of water quality change in the regional lakes was then compared with the rate of change in the Dorset lakes using analysis of similarities (ANOSIM, Clarke 1993). ANOSIM is a nonparametric test for multivariate differences between two or more groups. Rate-of-change values for the Dorset lakes were determined using Sen's slope, a nonparametric method that estimates the overall slope as the median of the slopes between each pair of time points (Sen 1968). ANOSIM was run in PAST (PAlaeontological STatistics) with 10 000 permutations (Hammer et al. 2001).

The above analyses assessed whether water quality in the regional lakes changed between sampling events and then compared the rate of change in the regional lakes with that in the Dorset lakes. To determine whether the directions of discrete changes in the regional lakes were consistent with monotonic trends in water quality over a continuous time period, temporal patterns in long-term data for the Dorset lakes were also examined. Water quality trends in the Dorset lakes between 1981 and 2005 were assessed using Regional Kendall trend tests implemented in Mystat 12 (Systat Software Inc. 2007). This nonparametric analysis was used to test for a consistent trend among the Dorset lakes, regardless of whether trends at individual lakes were significant (Helsel and Frans 2006). Trend test *p*-values were adjusted to account for possible autocorrelation (Hirsch and Slack 1984). The significance of trends in individual Dorset lakes were then assessed using Mann–Kendall trend tests (Hamed and Rao 1998).

Table 3. Summary of the number of lakes sampled each year during the two sampling periods and the number of years between sampling events for the 36 south-central Ontario regional study lakes.

No. of lakes	Year first sampled	Year resampled	Years between sampling events
1	1981	2005	24
8	1983	2004	21
7	1983	2005	22
9	1984	2004	20
3	1984	2005	21
1	1987	2004	17
4	1987	2005	18
1	1988	2005	17
2	1990	2004	14

Site-specific regulators of changes in water quality

The effect of lake and watershed characteristics on chemical change was examined using redundancy analysis (RDA), which is a multivariate ordination technique (Legendre and Legendre 1998). Descriptors were log or log(x + 1) transformed to meet RDA normality assumptions with the exception of $Z_{\max}$, ELEV, D_L, D_V, Q, DI, and RELIEF, which did not require transformation. Response values were the rate of water quality changes for all study lakes. Only water quality variables found to significantly differ between the two sampling periods (paired sample *t*-test *p*-values ≤ 0.05) were included. Linearity between rate-of-change values and lake and watershed descriptors was confirmed by detrended correspondence analysis prior to RDA (gradient lengths less than two). To reduce colinearity amongst the lake and watershed descriptors, a forward-selection step was included in the RDA and only variables with variance inflation factors of less than five were retained. Retained predictor variables were significant at $p \leq 0.05$ as determined by unrestricted Monte Carlo permutation tests (499 permutations). Monte Carlo permutations were also used to test the significance of the final ordination model. Two of the regional study lakes were excluded from the RDA. The first lake, Nunikani Lake, was excluded owing to missing watershed descriptors. The second lake, Glen Lake, was the only hardwater lake in the study and was identified as an outlier in a preliminary principal components analysis of the changes in water quality. Ordination analyses were performed using XLSTAT version 2010 (Addinsoft Inc. 2010).

Effect of interannual variability on changes in water quality

As the 36 regional study lakes were sampled across different years (Table 3), year-to-year variability within the sampling periods was a concern. Yearly fluctuations in factors such as weather can impact lake water quality, thus temporal changes may differ between groups of lakes sampled under different environmental conditions. Both mean air temperature and total precipitation varied over the sampling periods. During the 6 years that lakes were first sampled, temperatures ranged from 5 °C to 6.1 °C (average of 5.5 °C ± 0.4 °C), while precipitation ranged from 836 mm to 1165 mm (average of 1033 ± 140 mm). During the 2 years that lakes were resampled, temperatures averaged 5 °C ± 0.1 °C, but precipitation ranged greatly from 1067 mm in 2004 to 790 mm in 2005. To assess whether interannual variability in weather or other factors influenced water quality changes, two-way ANOSIM was used to compare the rate of change in subsets of regional lakes that were sampled in different years. In addition, one-way ANOSIM was used to compare the rate of change in the Dorset lakes for each combination of years that the regional lakes were sampled (Table 3). This allowed for the identification of any unusual year combinations.

Results

Temporal changes in water quality

Water quality changed in the 36 regional study lakes between the periods of 1981–1990 and 2004–2005 (Pillai's trace = 0.98, $F_{[22,14]} = 33.05$, $p < 0.001$). Fourteen of the 24 water quality variables that were examined changed over time ($p \leq 0.05$; Table 4), although changes in TP and Fe were not significant after FDR correction. Decreases in SO_4^{2-} were ubiquitous with a 2.2 μequiv.$\cdot$L$^{-1}\cdot$year^{-1} median rate of decline. Lake water pH and alkalinity increased, although the magnitude of the increases was less than expected based on SO_4^{2-} alone. During the first sampling period, 19 lakes had pH levels below 6. In 2004–2005, only 10 lakes remained at pH < 6, and 6 of these lakes contained high concentrations of organic acid (dissolved organic carbon > 6 mg$\cdot$L^{-1}). Decreases in the base cations Ca^{2+} and Mg^{2+} were also widespread, occurring in over 80% of lakes. The median rate of Ca^{2+} decline was 0.85 μequiv.$\cdot$L$^{-1}\cdot$year^{-1}, while median Mg^{2+} decline was 0.28 μequiv.$\cdot$L$^{-1}\cdot$year^{-1}.

Dissolved organic carbon increased in 35 of the regional study lakes with a median increase of 0.04 mg$\cdot$L$^{-1}\cdot$year^{-1}. The median change in $NH_3 + NH_4^+$ was 0.21 μg$\cdot$L$^{-1}\cdot$year^{-1} with 72% of the lakes increasing over time. Nearly 70% of the lakes decreased in TP and Chl *a* with median decreases of 0.3 and 0.2 μg$\cdot$L$^{-1}\cdot$year^{-1}, respectively, occurring in the regional lakes. The metals Fe and Mn^{2+} decreased in 67% and 75% of lakes, respectively, with Fe decreasing at a median rate twice that of Mn^{2+}. Na^+ and Cl^- increased in over 80% of the study lakes. Despite increases in Na^+ and Cl^-, conductivity decreased in 30 of the 36 regional study lakes.

The rate of change in water quality did not differ between the regional lake set and the Dorset lakes (ANOSIM $R = 0.06$, $p = 0.2$). Neither sampling year nor associated interannual variability in weather and environmental conditions affected the rate of change in water quality for the lake sets (ANOSIM p-values > 0.1). Water quality variables found to significantly increase or decrease over time in the regional study lakes were also consistent with 25-year trend data for the Dorset lakes with the exception of K^+ and Mn^{2+} (Table 4). Unlike the significant trend in the Dorset lakes, decreases in K^+ concentration for the regional lakes were not significant (paired *t*-test $p = 0.27$), although concentrations did decrease in 58% of the lakes. In the Dorset lakes, the trend in K^+ was negative, but concentrations increased above the long-term mean in 2004 and 2005 (Molot and Dillon 2008). If the same pattern of change occurred in the regional lakes, it may explain why K^+ did not significantly differ between the sampling events. Temporal changes in Mn^{2+} also differed between the regional and Dorset lakes as Mn^{2+} decreased in the regional study lakes (paired *t*-test $p = 0.003$), but the Dorset trend was not significant (Regional Kendall trend test $p = 0.2$). However, when trends in the Dorset lakes were assessed individually, Mn^{2+} decreased monotonically over time in four of the eight lakes, while concentrations increased in two of the remaining lakes (Mann-Kendall trend test p-values < 0.05).

Site-specific regulators of changes in water quality

The forward-selected lake characteristics (DI, ROADDIST, *Q*, and *V*) collectively accounted for 23% of the variance in the rate of water quality changes (ordination $p < 0.0001$; Table 5). The first RDA axis (explaining 16%) was positively correlated with lakeshore development and proximity to maintained roads (Fig. 2). This gradient separated developed lakes near roads from undeveloped lakes removed from maintained roads. Lakeshore development and road proximity were associated with greater increases in Na^+ and Cl^-, as well as smaller conductivity decreases in the study lakes (46%–52% of variance explained). The second RDA axis (explaining 7% of the variance in rate of change) was positively correlated with lake volume, runoff, and distance to road. This gradient separated small low-runoff lakes close to roads from large high-runoff lakes removed from roads. However, this gradient was not closely associated with the rate of change in any of the water quality variables (<20% of variance explained).

Discussion

The water quality of south-central Ontario lakes changed significantly over the 25-year period of 1981–2005. Temporal changes in water quality occurred at the regional scale, affecting lakes across a large gradient of lake and watershed characteristics and chemical statuses. The rate of change in water quality was similar between the 36 regional study lakes and the 8 long-term-monitoring Dorset lakes. This indicates that changes in the Dorset lakes were representative of regional shifts in water quality despite the limited variability and relatively small spatial extent of these lakes. As well, the direction of water quality changes in the regional lakes between 1981–1990 and 2004–2005 were generally consistent with 25-year temporal trends in the Dorset lakes, indicating that discrete changes in the regional lakes reflected long-term patterns of change. Observed multivariate changes were not an artefact of the sampling regime. Rather, the widespread shifts in water quality suggest that lakes were responding to changes in regional-scale stressors.

Improvements in lake water acidity occurred in response to a 50% reduction in SO_4^{2-} deposition between 1981 and 2005. Sulphate trends in the Dorset lakes closely mirrored deposition declines (Pearson correlation $r = 0.81$, $p < 0.0001$), indicating that regional changes were driven by deposition. As SO_4^{2-} decreased, lake alkalinity and pH increased in ~90% of the study lakes. The extent of improvements reported here are greater than those previously recorded for the region (Dillon and Evans 2000; Jeffries et al. 2003), likely owing to continued lake recovery as emissions remained below long-term means. Similar to the findings of McNicol et al. (1998) for small (<52 ha) Muskoka lakes, we found that recovery was slightly greater in acid-sensitive lakes because the median

Table 4. Summary of temporal changes in water quality for the regional and Dorset study lakes.

		Regional lakes (n = 36)						Dorset lakes (n = 8)						
			No. of lakes		Rate of change per year				No. of lakes			Rate of change per year		
Water quality variable	Units	Paired t-value	↑	↓	Median	Minimum	Maximum	Regional Kendall Z	↑	↓	No change	Median	Minimum	Maximum
Al	µg·L^{-1}	−1.11	13	23	−0.09	−4.95	1.77	1.39	1	2	5	0.22	−0.40	0.79
Alkalinity	µequiv.·L^{-1}	5.80**	32	4	0.62	−1.00	2.61	2.58*	6	0	2	0.19	−0.57	0.79
Ca^{2+}	µequiv.·L^{-1}	−5.85**	5	31	−0.85	−1.75	5.57	−3.37**	1	7	0	−1.00	−1.35	1.65
Chl *a*	µg·L^{-1}	−2.76*	11	25	−0.02	−0.29	0.19	−2.00*[a]	1	2	5	−0.02	−0.08	0.05
Cl^-	µequiv.·L^{-1}	3.25*	29	7	0.06	−0.24	5.85	3.26**	3	0	5	0.02	−0.03	6.58
Colour	TCU	1.11	21	15	0.05	−1.38	1.28	—	—	—	—	—	—	—
Conductivity	µS·cm^{-1}	−6.10**	6	30	−0.27	−0.45	0.43	−3.59**	0	7	1	−0.26	−0.31	0.59
DIC	mg·L^{-1}	1.19	18	18	0.00	−0.02	0.04	0.42	2	1	5	0.00	0.00	0.01
DOC	mg·L^{-1}	8.48**	35	1	0.04	−0.02	0.17	3.82**	6	0	2	0.03	0.00	0.06
Fe	µg·L^{-1}	−2.26*[a]	12	24	−0.74	−14.62	18.70	−3.40**	0	4	4	−1.35	−2.34	0.54
K^+	µequiv.·L^{-1}	**−1.11**	15	21	−0.01	−0.39	0.14	**−3.03***	0	5	3	−0.06	−0.15	0.02
Mg^{2+}	µequiv.·L^{-1}	−5.55**	4	32	−0.28	−0.62	2.36	−2.62*	1	6	1	−0.31	−0.44	0.40
Mn^{2+}	µg·L^{-1}	**−3.25***	9	27	−0.38	−3.79	0.85	**−1.24**	2	4	2	−0.21	−0.77	1.25
Na^+	µequiv.·L^{-1}	4.02**	34	2	0.26	−0.19	4.18	3.66**	3	0	5	0.10	0.03	3.98
$NH_3 + NH_4^+$	µg·L^{-1}	3.34*	26	10	0.21	−2.29	1.38	4.41**	7	0	1	0.68	0.22	1.32
$NO_2^- + NO_3^-$	µg·L^{-1}	−0.70	16	20	−0.24	−2.55	3.58	−1.13	0	1	7	−0.22	−1.51	0.22
pH	—	2.95*	35	1	0.01	0.00	0.03	2.98*	5	0	3	0.01	0.00	0.01
SiO_3^{2-}	µequiv.·L^{-1}	−0.56	17	19	−0.01	−1.32	0.67	−1.40	1	3	4	−0.12	−0.55	0.78
SO_4^{2-}	µequiv.·L^{-1}	−22.85**	0	36	−2.22	−5.53	−1.08	−4.68**	0	8	0	−1.84	−2.63	−1.42
TIN	µg·L^{-1}	0.18	19	17	0.17	−3.76	2.92	1.32	3	0	5	0.50	−0.98	0.89
TKN	µg·L^{-1}	0.09	18	18	0.02	−7.62	6.06	1.66	2	0	6	1.04	−0.75	2.12
TN	µg·L^{-1}	−0.17	14	22	−0.74	−7.33	5.98	0.78	2	0	6	0.48	−1.11	2.00
TON	µg·L^{-1}	−0.10	16	20	−0.20	−7.56	7.09	0.05	0	1	7	0.25	−1.20	1.07
TP	µg·L^{-1}	−2.03*[a]	12	24	−0.03	−0.48	0.29	−3.24**	0	5	3	−0.06	−0.10	0.00

Note: Arrows indicate the number of lakes with increasing or decreasing values over time. Changes significant at $p \leq 0.05$ (*) and 0.001 (**) are indicated. Bold type denotes changes that differ between the regional and Dorset lakes.

[a] Not significant after false discovery rate correction for multiple inferences.

Table 5. Redundancy analysis results relating water quality changes with forward-selected lake and watershed descriptors for the south-central Ontario study lakes.

	Axis 1	Axis 2
Eigenvalue	0.157	0.070
Water quality change and descriptors correlation	0.748	0.645
Cumulative water quality change variance explained (%)	15.7	22.7
Cumulative water quality change and descriptors variance explained (%)	51.5	74.6
Canonical coefficients		
Shoreline building density (DI)	1.169[a]	0.367
Distance to road (ROADDIST)	–0.715[a]	0.701[a]
Runoff (*Q*)	0.115	0.626[a]
Lake volume (*V*)	0.159	0.453[a]

[a]Significant at $p \le 0.05$.

rate of pH increase was 0.004·year^{-1} higher in lakes that were historically at pH ≤ 6 (two-tailed *t*-test $p = 0.05$). However, improvements in alkalinity and pH were tempered by widespread loss of lake Ca^{2+} and Mg^{2+}. In the regional lakes, 51% ± 24% of the decreases in SO_4^{2-} were balanced by Ca^{2+} and Mg^{2+} declines. These declines were due to long-term acidic leaching of catchment soils, which depleted the exchangeable cation reserves (Houle et al. 2006; Molot and Dillon 2008).

Although acidic deposition has had a moderate impact in south-central Ontario as compared with regions like Sudbury, Ontario (Dixit et al. 1992; Paterson et al. 2001), our findings demonstrate that anthropogenic acidification is still a primary determinant of water quality. In turn, water quality changes may impact lake biota. For example, 25% of the study lakes increased from pH < 6 to pH ≥ 6, which is a biologically significant threshold separating acidic and nonacidic lakes (Holt et al. 2003). As well, Ca^{2+} declines in Plastic Lake, one of the Dorset lakes, caused a severe decline in the relative abundance of *Daphnia*, which are keystone lake herbivores (Jeziorski et al. 2008). Recent laboratory work indicates that the minimum lake Ca^{2+} concentration required for daphniid survival and reproduction is between 25 and 75 μequiv·L^{-1} (Hessen et al. 2000; Ashforth and Yan 2008). Four lakes fell below 75 μequiv·L^{-1} during the study period. If Ca^{2+} continues to decline by 10%–40%, as predicted by model simulations of weathering rates (Watmough and Aherne 2008), the biota in up to 70% of lakes could be affected by low Ca^{2+}.

Climate change also impacted water quality in south-central Ontario lakes. As air temperature increases, organic matter production and decomposition, as well as DOC release from soils, are enhanced (Freeman et al. 2001; Keller et al. 2008). This DOC is then exported to lakes during subsequent precipitation events. Keller et al. (2008) suggested that this was the mechanism driving increases in DOC for the Dorset lakes. Between 1981 and 2005, long-term mean air temperature in the study region increased ~0.75 °C (Mann-Kendall trend test $p < 0.01$). During this period, the mean increase in DOC in the regional study lakes was 0.87 mg·L^{-1}, consistent with the estimate of Keller et al. (2008) that a 1 °C increase in air temperature would result in a 0.5–1.3 mg·L^{-1} increase in DOC.

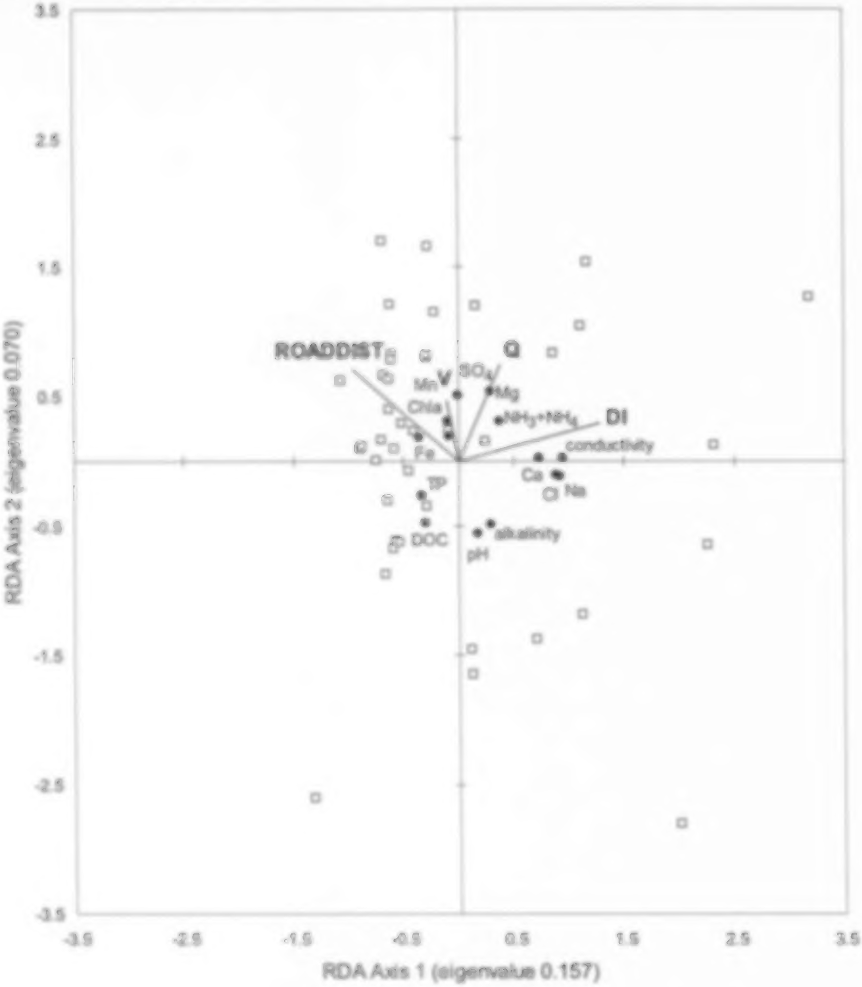
Climate change may also have contributed to increased $NH_3 + NH_4^+$, as trends in the Dorset lakes were positively correlated with long-term increases in mean air temperature (Pearson's correlation coefficient $r = 0.84$, $p < 0.0001$). Like DOC, terrestrial mineralization of ammonium may be enhanced during warm, dry periods (LaZerte and Scott 1996; Qiu and McComb 1996). Indeed, Watmough et al. (2005) proposed this as the mechanism driving increased $NH_3 + NH_4^+$ concentrations in two Dorset area streams between 1980 and 1999. The primary source of ammonium to lakes in the region is atmospheric deposition, since terrestrial retention of ammonium is extremely high (Kaste and Dillon 2003; Watmough and Dillon 2003). However, lake increases occurred between 1985 and 2000, concomitant with a period of relatively constant bulk deposition rates (Schindler et al. 2006). Similarly, anthropogenic nitrification likely does not explain recent increases, since agriculture and fertilizer use are limited and nitrogen inputs from shoreline development are generally low (Molot and Dillon 1993).

Lakeshore development and associated road salting were the likely drivers of increased lake Na^+ and Cl^- (Molot and Dillon 2008; Watmough and Aherne 2008). Localized use of road salt during the winter months is extensive in south-central Ontario (Henriksen et al. 2002) and NaCl is the most common form of road salt applied (District Municipality of Muskoka and FedNor 2004). Other road maintenance substances may also have contributed to ion accumulation. For example, $MgCl_2$ is used as a prewetting agent to reduce road salt scatter and $CaCl_2$ is used as a summer dust suppressant on gravel roads in some municipalities (District Municipality of Muskoka and FedNor 2004). Neary et al. (1990) reported that Na^+ levels > 50 μequiv.·L^{-1} and a strong relationship between Na^+ and Cl^- concentrations were strong indicators that a softwater lake had been impacted by road salt. Twelve of the study lakes had Na^+ levels ≥ 50 μequiv.·L^{-1} and the correlation between Na^+ and Cl^- increases was $r = 0.96$ ($p < 0.001$). In general, lakes close to roads and dense population centres had greater increases than lakes in more remote locations. Lakes close to roads may receive greater inputs of Na^+ and Cl^- following winter snowmelt, and road salt application is enhanced in populated areas, particularly if dwellings are used year round as opposed to seasonally. Despite recorded increases, Na^+ and Cl^- concentrations in the study region were among the lowest in Canada and were still an order of magnitude below biologically detrimental levels (Molot and Dillon 2008).

Conductivity also increased in developed lakes close to roads. This relationship was due to the high correlation between conductivity and Na^+ and Cl^- concentrations (regional lake Pearson correlation $r = 0.85$ and 0.86, respectively, *p*-values < 0.001). However, decreases in other ions, such as Ca^{2+}, caused conductivity to decrease regionally. Together, changes in Cl^- and Ca^{2+} explained 92% of the conductivity changes in the regional lakes (multiple linear regression $p < 0.001$).

Regional stressors driving changes in other water quality variables were less certain. Phosphorus decreased by almost 20% in the regional lakes. This was a significant loss in the predominately oligotrophic lakes and reductions resulted in lower Chl *a* levels (Pearson's correlation coefficient $r = 0.42$,

Fig. 2. Redundancy analysis ordination triplot displaying the forward-selected lake and watershed descriptors (solid lines and bold type) in relation to the study lakes (open squares) and the rate of change in water quality variables (solid circles). Descriptors and water quality variables corresponding to abbreviations displayed are shown in Table 2.



$p = 0.01$). Eimers et al. (2009) argued that reduced stream export during the spring was driving TP in the Dorset lakes. Phosphorus losses in the regional lakes also largely occurred in the spring. Reduced TP export was due to lower stream concentrations, suggesting processes that control terrestrial release of TP prior to and during spring snowmelt drove changes in export. Redox processes involving SO_4^{2-} and Fe could not explain TP changes (Eimers et al. 2009). Changes in lakeshore development and associated domestic waste production and fertilizer use, the primary sources of anthropogenic TP loading to lakes of the study region (Dillon et al. 1993), could also have affected lake water TP. However, TP decreased despite increased development (Eimers et al. 2009) and paleolimnological reconstruction of historical TP indicates cottage density and TP load are not correlated (Quinlan et al. 2008). As well, TP decreased at similar rates in both developed and undeveloped lakes. The mechanism causing decreased TP export may involve multiple stressors (Quinlan et al. 2008) and is the focus of current research (Eimers et al. 2009).

Similarly uncertain are the stressors driving regional decreases in Fe and Mn^{2+}. Sediment data suggest that long-range atmospheric transport of industrial emissions caused elevated metal deposition to lakes of the region (Dillon and Evans 1982; Evans et al. 1983). Thus, recent decreases in metal emissions may have contributed to declining metals (Mining Association of Canada 2003). Unfortunately, trends in metal deposition could not be assessed with available data. Changes in terrestrial export may also have contributed to metal decreases, particularly as stream water can be a primary source of metals (Adkinson et al. 2008). Previous studies have shown that Fe export is positively related to DOC export because Fe is strongly complexed by organic matter (Dillon et al. 1988; LaZerte 1991). However, Fe and DOC export were not correlated at Plastic Lake in 2002–2003 (Adkinson et al. 2008), and lake water Fe concentration decreased after the mid-1980s in two Dorset lakes despite constant DOC export (Eimers et al. 2008). As well, Fe and DOC trends in the Dorset lakes were inversely related over the current study period (Pearson's correlation coefficient $r = -0.42$, $p = 0.04$) and there was no correlation between Fe and DOC changes in the regional lakes ($p = 0.15$). These results indicate that declines in Fe were not driven by changes in DOC. Mn^{2+} export has been found to increase with SO_4^{2-} export (Adkinson et al. 2008), and Mn^{2+} and SO_4^{2-} were positively correlated in the four Dorset lakes in which Mn^{2+} decreased over the study period (Pearson correlation r between 0.5 and 0.8, p-values ≤ 0.02). However, Mn^{2+} and SO_4^{2-} were either not correlated or negatively correlated in the remaining Dorset lakes, all of which decreased in SO_4^{2-}. In addition, changes in Mn^{2+} and acidity variables were not correlated in the regional study lakes (p-values > 0.1), indicating that acidification did not cause changes in Mn^{2+}. Another stressor that may have affected metal concentrations was climate change. Dillon and Molot (2005) found that Fe export to the Dorset lakes was reduced under warm temperatures with reduced runoff, while Adkinson et al. (2008) found that export of metals, such as Mn^{2+}, from a wetland at Plastic Lake increased following prolonged droughts, perhaps owing to SO_4^{2-} enhanced metal mobilization. The stressors driving temporal changes in Fe and Mn^{2+} are currently unknown but may involve complex interactions between a warming climate, DOC, and acidity.

The large spatial extent of water quality changes combined with correlation-based evidence indicate that south-central Ontario lakes have changed in response to regional stressors, particularly changes in acidic deposition, climate, and the use of road salt. Individual lake responses to these stressors differed, suggesting that change was regulated by site-specific factors. However, differential lake responses were largely unrelated to the examined lake and watershed characteristics. This was surprising, as stressor-induced changes in water quality have previously been related to local factors, such as hydrology (Arnott et al. 2003; Quinlan et al. 2003). The lake and watershed characteristics chosen for examination were those known to influence lake chemistry. Our results suggest that these characteristics had a much more limited role in determining lake responses to stress. Other lake and watershed descriptors that were not available for this study, such as wetland area, may have influenced lake responses to stress. Perhaps of greater importance was lake history (e.g., Bleckner 2005), including lake chemistry prior to the onset of current stressors. For example, Hall and Smol (1996) found that lake response to acidification was dependent upon the initial chemical composition of a lake. The effect of predisturbance chemistry on lake response to stress could not be assessed in this study because the first sampling event (1981–1990) coincided with a period of rapid transition in the study lakes (M.E. Palmer, unpublished data), making it difficult to assess the initial chemical composition of the lakes. Future work is needed to identify the factors that regulate individual lake responses to regional stressors.

Water quality in south-central Ontario lakes has changed extensively over the last 25 years. Reductions in acidic deposition resulted in reduced lake acidity, although loss of base cations limited improvements in lake alkalinity and pH. Climate warming increased DOC export to lakes and may have contributed to increased $NH_3 + NH_4^+$ concentrations. Residential development and road salting caused Na^+ and Cl^- to increase. As well, TP and metals have decreased over time. Temporal changes in water quality were generally consistent between the 36 diverse regional study lakes and the 8 long-term-monitoring Dorset lakes. Our findings indicate that the Dorset lakes are reliable sentinels of water quality responses to regional stressors in south-central Ontario.

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Benthic and pelagic contributions to *Mysis* nutrition across Lake Superior

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Abstract: Quantifying nutritional sources for *Mysis diluviana* will help to clarify the basis for production in lakes with *Mysis* and improve models of migration-driven nutrient and contaminant transport. We sampled *Mysis*, plankton, and benthos across Lake Superior using a stratified-random design that provided a statistically valid representation of the lake across depths. We then estimated nutritional contributions to *Mysis* using stable isotope ratios of *Mysis*, zooplankton, *Bythotrephes*, *Diporeia*, oligochaetes, and detritus in a multiple-source, dual-isotope mixing model. Lake-wide, small (<1.0 cm) mysids relied almost exclusively upon plankton, whereas large mysids occupied a higher trophic position and obtained nutrition among sources. Model estimates of mean benthic contributions to large *Mysis* ranged from 27% to 58%. We predicted the importance of benthos to *Mysis* to track declining benthic biomass with depth. Model results indicated that if *Diporeia* were the only benthic food eaten, benthic contributions would decline to 40% with depth, but inclusion of detritus in the model resulted in consistent importance of benthic food across depths. The importance of benthos to mysid nutrition suggests strong benthic–pelagic coupling at all lake depths and might limit the ability of *Mysis* to support fisheries in systems that have lost *Diporeia*.

Résumé : L'analyse quantitative des sources de nourriture de *Mysis diluviana* va aider à clarifier la base de la production dans les lacs à *Mysis* et améliorer les modèles de transport des nutriments et des contaminants basés sur la migration. Nous avons échantillonné les *Mysis*, le plancton et le benthos à travers le lac Supérieur selon un plan stratifié-aléatoire qui fournit une représentation statistiquement valide du lac en fonction des profondeurs. Nous avons ensuite estimé les contributions alimentaires aux *Mysis* en utilisant les rapports d'isotopes stables des *Mysis*, du zooplancton, de *Bythotrephes*, de *Diporeia*, des oligochètes et du détritus dans un modèle de mélange de deux isotopes à sources multiples. À l'échelle du lac, les petits (<1,0 cm) *Mysis* dépendent presque exclusivement du plancton, alors que les grands *Mysis* occupent une position trophique plus élevée et obtiennent leur nourriture de différentes sources. Les estimations par le modèle des contributions moyennes du benthos aux grands *Mysis* varient de 27 % à 58 %. Nous avons prédit que l'importance du benthos aux *Mysis* suit la biomasse benthique qui diminue en fonction de la profondeur. Les résultats du modèle indiquent que si *Diporeia* était le seul aliment benthique consommé, les contributions du benthos diminueraient de 40 % en fonction de la profondeur; cependant, l'inclusion du détritus dans le modèle résulte en une importance soutenue des aliments benthiques à toutes les profondeurs. L'importance du benthos dans l'alimentation des *Mysis* laisse penser qu'il existe un fort couplage benthique–pélagique à toutes les profondeurs du lac; elle peut aussi limiter la capacité des *Mysis* à soutenir les pêches dans les systèmes qui ont perdu les *Diporeia*.

[Traduit par la Rédaction]

Introduction

Understanding the role of *Mysis* in lake food webs continues to be an important and fertile area of research. In the Laurentian Great Lakes, *Mysis diluviana* (formerly *Mysis relicta*) is an important food organism for most fish species (Anderson and Smith 1971; Hudson et al. 1995; Owens and Dittman 2003) and a voracious consumer with omnivorous feeding habits (e.g., Bowers and Vanderploeg 1982; Grossnickle 1982; Johannsson et al. 2001). Its presence in lakes can structure invertebrate and consumer communities (Goldman et al. 1979; Nero and Sprules 1986; Chipps and Bennett 2000). Mysid introductions intended to bolster the forage base for fish, but made with an insufficient understanding of the powerful role mysids play in food webs, have produced strong and unforeseen results in North American and European lakes (Kinsten and Olsen 1981; Rieman and Falter 1981; Lasenby et al. 1986). The presence of mysids can increase food chain length and, therefore, increase contaminant burdens in top predators (Cabana and Rasmussen 1994; Bentzen et al. 1996; Vander Zanden and Rasmussen 1996). *Mysis*' nocturnal vertical migrations into the metalimnion hold strong implications for benthic–pelagic coupling, influencing the mobilization of contaminants and nutrients. *Mysis* accumulates and transports benthic metals (Van Duyn-Henderson and Lasenby 1986; Song and Breslin 1999) and

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organic contaminants (Klump et al. 1991; Lester and McIntosh 1994; Bentzen et al. 1996) into pelagic food web pathways. Mysid body size, amount of benthic feeding, and ontogenetic feeding shifts were predicted to govern contaminant body burdens in *Mysis* and upper trophic level organisms in a bioaccumulation model (Patwa et al. 2007). Excretion by *Mysis* during their metalimnetic forays releases nutrients that become available for algal uptake and may supply as much as 10% of algal demands in subthermocline algal maxima (Madeira et al. 1982; Chipps and Bennett 2000; Lindén and Kuosa 2004).

Most studies of feeding by *Mysis* have focused on its nocturnal metalimnetic feeding, but planktivory alone may not satisfy *Mysis*' bioenergetic requirements (Johannsson et al. 1994). This suggests that substantial nutrition may be obtained from benthic sources. Benthic feeding, which mostly occurs during the daytime when *Mysis* is at or near the sediments, is known to include the amphipod *Diporeia* spp. (Green 1965; Parker 1980; Johannsson et al. 2001) and sedimented detritus (Klump et al. 1991; Lasenby and Shi 2004). Whereas rates of planktivory by *Mysis* have been measured under natural conditions in the Great Lakes (e.g., Bowers and Vanderploeg 1982), the difficulties in measuring benthivory in situ have hampered its quantification. Here we combine stable isotope analyses of *Mysis* and its foods with an isotope mixing approach to present the first lake-wide estimates of benthic and planktonic nutrition for adult and juvenile *Mysis*. These estimates of the proportion of *Mysis*' nutrition deriving from different sources should greatly improve our understanding of the role of *Mysis* in food webs, as well as estimates of nutrient and contaminant transport by *Mysis*.

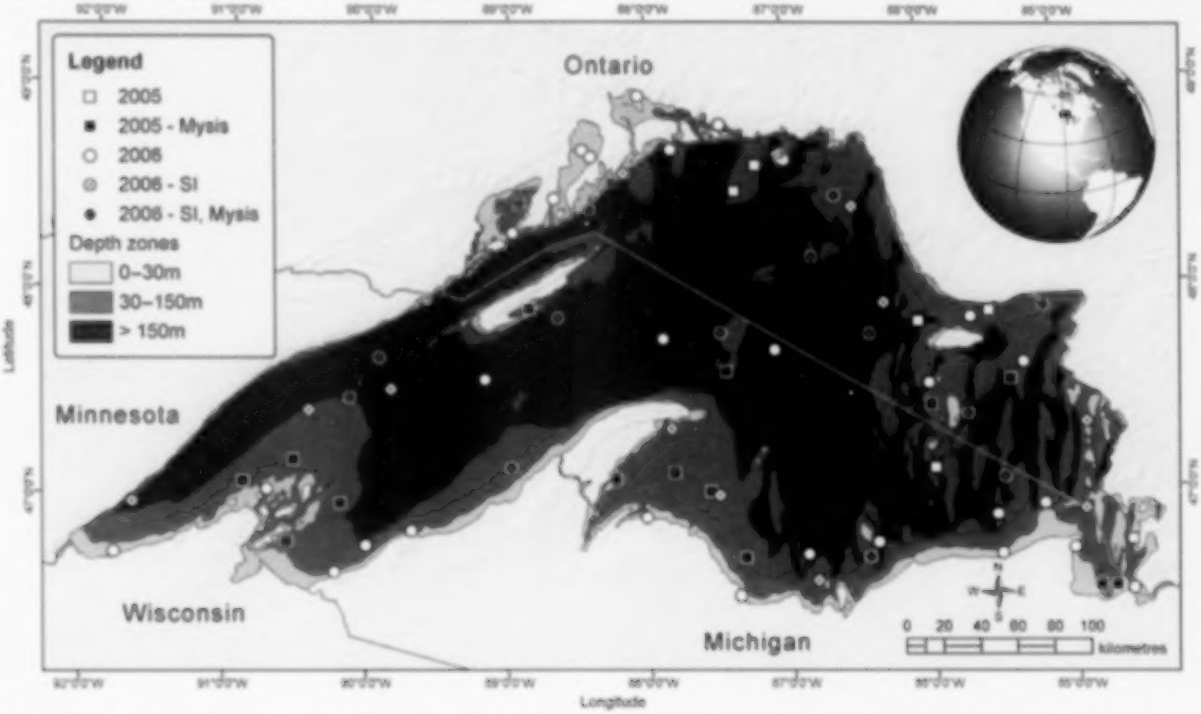
Despite introductions of non-native species, the food web structure of Lake Superior is relatively unchanged from historic times (Schmidt et al. 2009). In contrast with the lower Great Lakes, the food web of Lake Superior is comparatively stable, and populations of native benthic invertebrates, dominated by *Mysis* and the amphipod *Diporeia* spp., remain healthy (Scharold et al. 2004; 2009). By understanding the role of *Mysis* in Lake Superior, we may better understand its role in intact systems, and we may also better predict the consequences of food web disruption and management actions in disturbed systems. In Lake Superior, *Diporeia* abundance peaks at 40–70 m depth (up to 5000 animals·m^{-2}) and declines beyond 70 m depth to 200–300 animals·m^{-2} in profundal regions (Scharold et al. 2004, 2009; Auer et al. 2009). Abundances of other benthic taxa similarly decline in the profundal zone (Cook 1975; Dermott 1978; Auer and Kahn 2004). Food quality of benthic detritus declines in deep zones because sedimenting particles have decomposed by the time they reach the sediments (Eadie et al. 1984; Ostrom et al. 1998), which is likely the cause of low zoobenthos numbers there (Mozley and Howmiller 1977; Evans et al. 1990). In contrast, *Mysis* abundance increases with depth and remains high in even the deepest regions of the Great Lakes (Sell 1982; Johannsson 1995; Pothoven et al. 2004). These patterns suggest that the relative importance of benthic nutrition to *Mysis* might decline with depth.

Stable isotope techniques provide a way to quantify nutritional contributions from food sources that differ in their isotopic signatures. In Lake Superior, nitrogen isotope ratios ($\delta^{15}N$) of *Diporeia* increase by approximately 4‰ from nearshore (40 m) to deepwater (300 m) stations, whereas $\delta^{15}N$ of plankton remains constant with water column depth and ^{15}N-depleted relative to *Diporeia* by 3‰–7‰ (Sierszen et al. 2006). Progressive isotope enrichment of benthos with depth occurs through a combination of processes. As detritus sinks, decomposition causes release of light isotopes, and the residual detritus becomes progressively ^{15}N-enriched as it sinks (Saino and Hattori 1985; Ostrom et al. 1998). Colonization by bacteria, which effectively add a higher trophic level and therefore higher isotope ratios to the detrital particles, undoubtedly contributes to isotope enrichment. Zoobenthos that feed upon that sedimented detritus therefore also become ^{15}N-enriched with depth (Sierszen et al. 2006). One would expect, therefore, that planktivores should have relatively constant $\delta^{15}N$ values regardless of where they are collected, while benthivores (at least those that do not forage widely among depths) should, like their food, have increasing $\delta^{15}N$ with depth. If an omnivore such as *Mysis* obtained nutrition from a combination of benthic and planktonic sources, we would expect its $\delta^{15}N$–depth relationship to have an intermediate slope. We used those baseline patterns in nitrogen isotope signatures, together with carbon isotope ratios, to calculate depth-specific estimates of benthic and planktonic contributions to the nutrition of *Mysis* in Lake Superior.

Materials and methods

We sampled *Mysis*, benthos, and plankton across Lake Superior in September of 2005 and 2006 (Fig. 1) using a stratified-random sampling design that provided a statistically valid representation of the lake across three depth zones (0–30, 30–150, >150 m). Sampling sites for both 2005 and 2006 were selected using a generalized random tessellation stratified survey design (Diaz-Ramos et al. 1996; Stevens and Olsen 1999, 2004). This approach provides a random, unbiased selection of sites and includes reverse hierarchical ordering to achieve spatial balance in distribution of sites across the area of interest. This style of survey design has come to be known as spatially balanced sampling (Theobald et al. 2007). The lake was stratified into offshore (>150 m water depth) and nearshore (0–150 m) depth zones, with the nearshore further partitioned into shallow (0–30 m) and medium depth (30–150 m) zones prior to site selection. In general, we intended to sample more sites in nearshore waters, as we expected variability to be highest there and wanted more sampling to overcome this variability. In 2005 we sampled 20 medium depth zone sites for *Diporeia*, of which 14 were sampled at night to facilitate capture of *Mysis* in the water column. At three of the 20 sites, insufficient *Diporeia* were captured for stable isotope analysis. In 2006 we exercised a lake-wide design of 52 total sites for enumeration of plankton, benthos, and other parameter measurements (cf. Yurista et al. 2009). Of those, a subset of 25 stations was selected for plankton and benthos stable isotope sampling. It was necessary to limit *Mysis* sampling to a smaller subset that could be sampled at night to enable an efficient overall survey. We were able to sample a *Mysis* subset of 14 sites, with target sites in both the offshore and medium depth zones. Previous studies have shown low *Mysis* abundance at shallow depths; for this and vessel safety during night operations, we excluded the shallow

Fig. 1. Map of Lake Superior, showing the three sampling depth zones and sampling stations: open squares, 2005 stations; filled squares, 2005 *Mysis* stations; open circles, 2006 stations; crossed open circles, stable isotope stations; crossed filled circles, 2006 *Mysis* stations. Inset shows location in the Great Lakes region of North America.



nearshore zone (<30 m) from *Mysis* sampling. The 2006 *Mysis* subset was nested within the overall lake-wide design such that it too represented a (smaller) random, unbiased selection. We have used the combined 2005–2006 sites to provide the lake-wide coverage in the *Mysis* analyses presented here. Several sites were slightly deeper than expected because of imperfection in the GIS–bathymetry frame used for selection; a total of 8 sites exceeded 150 m (offshore zone) and 20 were in the 30–150 m (medium depth zone) range.

Mysis were collected after dark using vertical tows with a 1 mm mesh plankton net with a 1 m^2 mouth area, raised at a rate of 0.3 $m \cdot s^{-1}$. All white deck and cabin lights were turned off, and red lights were used for illumination. Tows were from 100 m to the surface or, at stations less than 100 m depth, from 5 m above bottom to the surface. This captured mysids after their nocturnal vertical migration to feed in the subthermocline deep chlorophyll maximum (DCM), when they concentrate near 50 m depth (Jensen et al. 2009). Although a portion of the Lake Superior *Mysis* population may not migrate every night (Bowers 1988; Jensen et al. 2009), the nonmigratory portion consists of all instars (Bowers 1988). We therefore believe that our samples represented the breadth of mysid size classes present in the Lake Superior population. Four tows were taken at each station for enumeration of *Mysis*, and additional tows were taken to obtain mysids for isotope analysis. Each sample taken for enumeration was preserved in 10% buffered formalin. Mysids were rinsed, placed in a dissecting dish, counted, and photographed with a SMZU Nikon dissecting microscope mounted with a Nikon 5m digital camera. Microsoft Image Pro 6.1 software (Media Cybernetics, Inc., Bethesda, Maryland) was used to measure each mysid from the digital photos to the nearest 0.1 mm. Length was measured from the tip of rostrum to end of the telson. For samples with ≤100 individuals, all were counted and measured. For samples with more than 100 individuals, 100 haphazardly selected individuals were measured, and the remaining individuals were grouped by size and counted. Samples for isotope analysis were rinsed in 1 $mol \cdot L^{-1}$ HCl and deionized water, then frozen pending analysis. Prior to isotope analysis, *Mysis* were separated into three sizes according to Branstrator et al. (2000), who found $\delta^{15}N$ differences among *Mysis* <1, 1–1.5, and >1.5 cm in Lakes Michigan, Huron, Champlain, and Memphramagog.

Plankton were collected at all 2006 sites using a 0.5 m diameter, 63 μm mesh plankton net towed from 50 m depth to the surface to capture plankton from the DCM, where the majority of phytoplankton and zooplankton biomass is found in offshore waters (Yurista et al. 2009). Plankton were sampled after dark just after mysid sampling to ensure that the samples captured a representative DCM prey assemblage. We divided plankton samples into large (>160 μm) and small (63–160 μm) size fractions using Nitex sieves and identified the contents of each size fraction microscopically. We picked the invasive predatory cladoceran *Bythotrephes longimanus* from the large size fraction zooplankton and stored and analyzed it separately. Samples of plankton for stable isotope analysis were not collected in 2005.

To estimate planktonic biomass available to mysids, we used zooplankton biomass measurements from Yurista et al. (2009). Those estimates were made using LOPC (laser optical plankton counter) tows through the water column during the 2006 cruise, which were calibrated by flow-meter-corrected plankton net tows at the sampling stations. The data presented in Yurista et al. (2009) were as dry mass; to make them comparable to our benthic biomass estimates, we converted zooplankton data to wet mass using a 10:1 wet–dry conversion factor (P.M. Yurista, unpublished data).

We collected benthic invertebrates at all 2005 and 2006 sites with a PONAR grab (area = 0.046 m^2; sediment sample depth ~10 cm) immediately after mysid and plankton sampling. We present abundance data from 2006 and stable isotope data from both 2005 and 2006. At each station, triplicate grabs were taken for enumeration of benthos, and additional grabs were taken to obtain enough organisms for isotope analysis. Samples were elutriated in a basin with a 500 μm mesh sleeve on the outlet. The residue containing the organisms for enumeration was preserved with 5% formalin containing Rose Bengal stain. To determine the amount of benthic prey biomass available for *Mysis* as a function of depth, organisms were separated from each sample under a dissecting microscope and sorted into families, except for oligochaetes, which were grouped together. For each sample, biomass was determined as wet mass of organisms in each group, measured to the nearest 0.01 mg. Values from the three grabs were averaged for each station. For stable isotope samples, organisms of sufficient abundance for isotope analysis (*Diporeia* and oligochaetes) were picked from the retained material and placed into 47 mm diameter Petri dishes. Unlike *Diporeia*, oligochaetes have not been described as a food item for *Mysis*. However, the opportunistic nature of *Mysis*' feeding suggests that oligochaetes could be a potential prey. *Diporeia* accounts for 50%–61% of Lake Superior benthos by abundance; oligochaetes (mostly *Stylodrilus heringianus*) account for 22%–27%; fingernail clams (*Pisidium*), which are inedible by *Mysis*, account for 14%–16%; and chironomids account for only 3%–5% (Scharold et al. 2009). Therefore, by including *Diporeia*, oligochaetes, and detritus in our analyses, we have included the most important benthic foods. All organisms were rinsed with 1 mol·L^{-1} HCl and deionized water and frozen pending analysis.

We analyzed the samples for carbon and nitrogen isotope ratios on a Micromass Isochrom-EA C2500 isotope ratio mass spectrometer (GV Instruments, Manchester, UK). Isotope ratios are expressed as δ values, parts-per-thousand deviations from the ratios found in reference materials (PeeDee Belemnite C and atmospheric N). Samples enriched with the heavier isotope have δ values that are relatively more positive. We quantified contributions to *Mysis*' nutrition using our measurements of large and small plankton, *Diporeia*, *Bythotrephes*, and oligochaete isotope ratios in a multisource, dual-isotope mixing model (IsoSource 1.3.1; Phillips and Gregg 2003; Phillips et al. 2005). IsoSource is an iterative probabilistic model that calculates source contributions to a stable isotope mixture when the number of sources is too large to permit a unique solution (i.e., number of sources > number of isotope systems + 1). All possible combinations of each source are examined in small increments, and combinations that sum to the observed mixture within a small tolerance (here, 0.1‰) are considered to be feasible solutions. Possible combinations are reported as mean and standard deviation of each source's probable contribution. We used linear regression to test for significant changes in isotope signatures with station depth. Because we did not have each sample type at every sampling station, we used significant regressions to estimate δ^{15}N and δ^{13}C of *Mysis* and food items at 50 m intervals and used those predictions in the mixing model. For nonsignificant regressions, we used mean isotope ratios. *Mysis* is known to feed upon sedimented detritus (Klump et al. 1991; Lasenby and Shi 2004), and to represent recently sedimented organic-rich material (Urban et al. 2004), we used measurements of the isotope ratios of the benthic nepheloid layer (BNL) in Lake Superior (Ostrom et al. 1998). δ^{15}N of the BNL increased with depth (1.7‰ at 120 m, 2.7‰ at 200 m, and 3.3‰ at 300 m), and we used linear regression to predict values at 50 m intervals. BNL δ^{13}C did not change systematically with depth (–29.1‰ at 120 m, –28.3‰ at 200 m, and –28.5‰ at 300 m); thus we used the average value (–28.63‰) in the mixing model (Ostrom et al. 1998). Calculating isotope mixing across trophic levels requires that trophic fractionation of isotopes, the ^{15}N and ^{13}C enrichment of a consumer relative to its food, be known. We used a nitrogen isotope fractionation factor of 2.2‰ and carbon isotope fractionation of 0‰ for *M. diluviana* (Johannsson et al. 2001).

To examine the mixing model responses to variations in potential food sources, we compared predictions of total benthic contributions with large and small mysids under scenarios ranging from a simple three-source solution (*Diporeia*, small zooplankton, large zooplankton) to a six-source solution (small zooplankton, large zooplankton, *Diporeia*, BNL, *Bythotrephes*, and oligochaetes).

Results

Number of *Mysis* captured in net tows increased with depth, and small mysids greatly outnumbered large mysids in depths greater than 140 m, reaching 160 small mysids·m^{-2} (Fig. 2). Integrated water column biomass of zooplankton (g wet mass·m^{-2}) increased with water depth, reaching 15–20 g·m^{-2} at depths greater than 150 m (Fig. 3). The vertical structure in zooplankton biomass revealed by LOPC tows showed peak biomass near the thermocline at about 20–30 m in late summer (see figure 5*b* in Yurista et al. 2009). Plankton large size fractions were dominated by *Holopedium*, diaptomid copepods, and *Bythotrephes*, the latter of which were analyzed separately for stable isotopes. Small size fractions contained a mixture of diatoms, rotifers, and nauplii. Total biomass of benthic invertebrates peaked at approximately 10 g wet mass·m^{-2} in nearshore depths of 40–60 m and declined steadily with depth. *Diporeia* biomass followed a similar distribution and provided a large portion (averaging 53%) of the total benthic biomass, especially in depths less than 100 m (Fig. 3).

Among the three size categories of *Mysis* analyzed (<1, 1–1.5, and >1.5 cm), there was no statistical difference between the δ^{15}N of 1.0–1.5 and >1.5 cm sizes (analysis of variance (ANOVA) with depth as covariate; $n = 42$, $F = 2.3$, $p = 0.14$). We therefore pooled those groups and henceforth refer to small (<1 cm) and large (>1 cm) *Mysis* size classes. Pooling 2005 and 2006 mysid data was justified as there were no

Fig. 2. Mean (±1 standard deviation) abundance (animals·m^{-2}) of large (closed circles) and small (open circles) *Mysis* captured in night tows versus depth of sampling station.

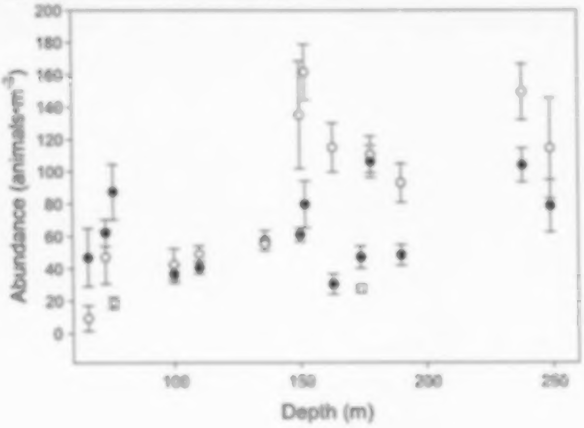
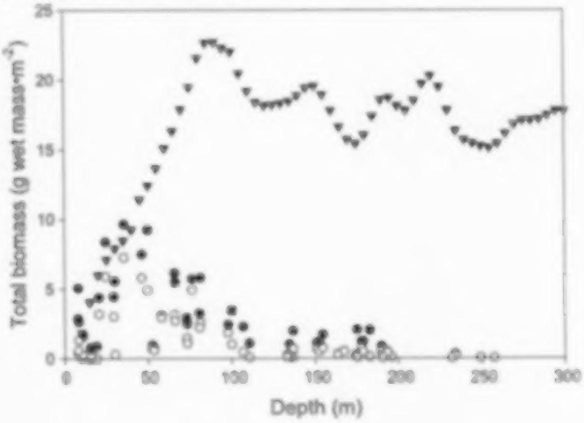
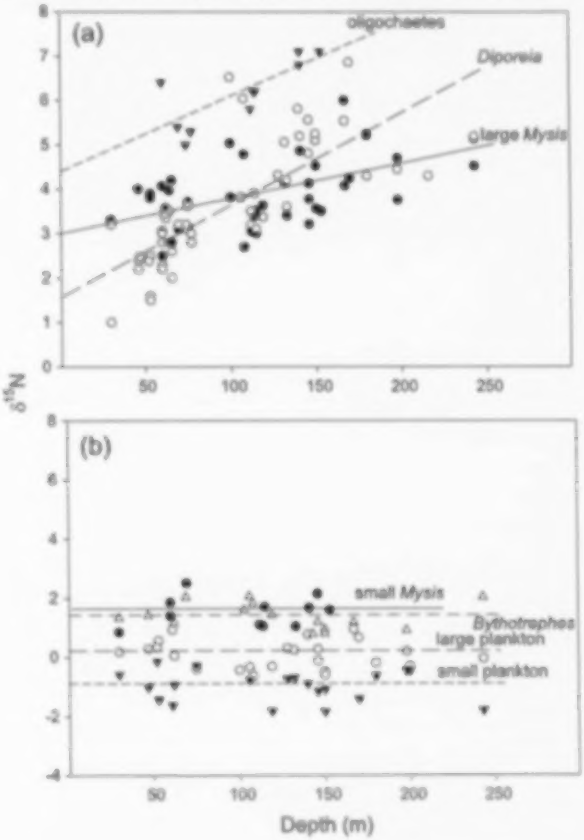


Fig. 3. Total water column biomass (g wet mass·m^{-2}) of benthic invertebrates (combined *Diporeia*, oligochaetes, and chironomids: closed circles), *Diporeia* only (open circles), and zooplankton (triangles) versus water column depth.



significant differences between years for either δ^{15}N or δ^{13}C (ANOVA with depth as covariate; $F = 2.298$, $p = 0.14$ for δ^{15}N; $F = 0.253$, $p = 0.62$ for δ^{13}C). As found earlier (Sierszen et al. 2006), δ^{15}N of *Diporeia* increased with depth (Fig. 4*a*). Within the range of depths sampled in this study, the increase in *Diporeia* δ^{15}N with depth was linear according to the relationship $\delta^{15}N = 1.6749 + 0.0198 \times d$, where d is water column depth in metres ($n = 50$; $F = 59.05$; $p < 0.0001$). Oligochaete δ^{15}N was ^{15}N-enriched by approximately 2.5‰ relative to *Diporeia*. Unlike *Diporeia*, which feeds upon freshly sedimented material at the sediment surface, oligochaetes feed below the sediment–water interface (Robbins et al. 1984). They therefore ingest bacteria and more thoroughly decomposed detritus than *Diporeia* and become more isotopically enriched than *Diporeia*. Oligochaete δ^{15}N also increased with depth, following the relationship $\delta^{15}N = 4.2916 + 0.0174 \times d$ ($n = 12$; $F = 12.63$; $p = 0.0075$). δ^{15}N of large *Mysis* increased significantly with depth, indicating a significant benthic component in their diet, but the slope of the increase was not as steep as those for *Diporeia* or oligochaetes. δ^{15}N of large *Mysis* was ^{15}N-depleted relative to *Diporeia* at shallow stations but became ^{15}N-enriched relative to *Diporeia* in deeper waters, according to the relationship $\delta^{15}N = 2.9744 + 0.0078 \times d$ ($n = 42$; $F = 15.83$; $p = 0.0003$). Small *Mysis* had lower δ^{15}N than large *Mysis*, indicating a lower trophic position. δ^{15}N of small *Mysis*, *Bythotrephes*, and both zooplankton size fractions were statistically invariant with depth (Fig. 4*b*). For small *Mysis*, the two zooplankton size fractions, and *Bythotrephes*, we therefore used their mean δ^{15}N values in the isotope mixing model. Calculated mean (standard deviation) δ^{15}N values for groups with nonsignificant regressions were as follows: small *Mysis*, 1.54 (0.51); small zooplankton, –0.99 (0.52); large zooplankton, 0.075 (0.47); *Bythotrephes*, 1.38 (0.44). Small-fraction zooplankton had negative nitrogen isotope ratios because the nitrogen source in Lake Superior, nitrate, has a

Fig. 4. (*a*) δ^{15}N of large *Mysis* (closed circles), *Diporeia* (open circles), and oligochaetes (triangles); (*b*) δ^{15}N of small *Mysis* (closed circles), *Bythotrephes* (open triangles), large zooplankton (open circles), and small plankton (triangles) in Lake Superior. Also shown are linear regressions of δ^{15}N versus depth for each food web component. All regressions in panel (*a*) are statistically significant. Note the difference between panels (*a*) and (*b*) in scale of vertical axis.



very low isotope ratio, averaging –4.1‰ (Ostrom et al. 1998).

Diporeia was the only food web component in which measured $\delta^{13}C$ changed significantly with depth. *Diporeia* $\delta^{13}C$ increased with depth according to the relationship $\delta^{13}C = -27.6594 + 0.0112 \times d$ ($n = 42$; $F = 13.33$; $p = 0.0006$). Calculated mean (standard deviation) $\delta^{13}C$ values for groups with nonsignificant regressions were as follows: small *Mysis*, –25.36 (0.62); large *Mysis*, –26.10 (0.92); small zooplankton, –24.51 (1.42); large zooplankton, –26.82 (1.10); oligochaetes, –24.35 (0.91); *Bythotrephes*, –26.00 (0.77). Even though $\delta^{13}C$ did not discriminate among taxa as well as $\delta^{15}N$ because of the overlap in $\delta^{13}C$ among taxa and relative lack of pattern with depth, the use of both $\delta^{13}C$ and $\delta^{15}N$ in the mixing model resulted in lower estimates of error than were obtained using only $\delta^{15}N$.

Trophic fractionation of nitrogen isotopes often averages approximately 3.4‰ per trophic level across whole food webs (DeNiro and Epstein 1981; Cabana and Rasmussen 1994; Hobson and Welch 1995). However, isotope fractionation by individual species can vary, and our results help to provide nitrogen trophic fractionation values that will be useful in trophic studies of *Mysis* and *Bythotrephes*. We assumed that even though fractionation may vary somewhat according to food items (e.g., Gorokhova and Hansson 1999), most variability would be determined by the physiology of the consumer (Vander Zanden and Rasmussen 2001). We therefore used constant fractionation values for feeding by *Mysis* in our analyses. We obtained reasonable mixing results by using the nitrogen trophic fractionation value of 2.2‰ for *M. diluviana* suggested by Johannsson et al. (2001). We found that if we used fractionation values greater than 2.5‰, no mixing solutions were possible. Our results therefore support the use of a 2.2‰ fractionation factor for *Mysis*.

Although we did not examine feeding by *Bythotrephes*, our data can be used to empirically obtain an estimate of trophic fractionation for *Bythotrephes* by comparing our measurements of *Bythotrephes* and zooplankton $\delta^{15}N$. *Bythotrephes* has been found to feed selectively upon large cladocerans and copepods (Yurista and Schulz 1995; Schulz and Yurista 1999). The difference between average $\delta^{15}N$ of *Bythotrephes* (1.38‰) and large-fraction zooplankton (0.08‰) was 1.30‰. The mean (standard deviation) difference calculated station-by-station was 1.28‰ (±0.65). We therefore suggest a nitrogen isotope trophic fractionation factor for *Bythotrephes* of 1.3‰. Error in this estimate may stem from selective feeding by *Bythotrephes* upon the taxa included in the large size fraction. If *Bythotrephes* selected herbivorous cladocerans (e.g., Dumitru et al. 2001), which would have lower $\delta^{15}N$ than the omnivorous diaptomid copepods also in the samples (e.g., Matthews and Mazumder 2003), actual trophic fractionation might be greater than our estimate. An upper limit might be set at the difference between *Bythotrephes* (1.38‰) and the average value for small-fraction plankton (–0.99‰), or 2.37‰. However, in the absence of knowledge at this level of detail, we tentatively suggest a value of 1.3‰.

Because a very broad body of work has shown that *M. diluviana* feeds extensively upon phytoplankton (e.g., Bowers and Grossnickle 1978; Grossnickle 1982; Johannsson et al. 2001), zooplankton (e.g., Bowers and Vanderploeg 1982; Johannsson et al. 2001), *Diporeia* (Green 1965; Parker 1980; Johannsson et al. 2001), and detritus (e.g., Lasenby and Langford 1973; Klump et al. 1991; Lasenby and Shi 2004), we present as a general model the mixing model results using four sources: small-fraction plankton (which included diatoms, rotifers, and nauplii), large-fraction plankton (dominated by cladocerans and diaptomid copepods), *Diporeia*, and BNL (Fig. 5*a*). Results indicated that nutrition to large *Mysis* was distributed broadly across food sources. Mean contributions from the different sources varied with depth, as major contributions from small-fraction plankton and *Diporeia* at 50 m graded to a more even distribution at 250 m (Fig. 5*a*). Consistent with predictions based upon declining abundance of benthos with depth, contributions by *Diporeia* declined from 55% at 50 m to 36% at 250 m. However, contributions by BNL increased with depth so that total benthic contributions remained consistent at ~55% (Fig. 5*b*). Similarly, tradeoffs between the contributions of small- and large-fraction plankton (Fig. 5*a*) kept total planktonic contributions consistent at ~45% (Fig. 5*b*). The four-source solution (Fig. 5*a*) predicts possible switches in feeding by *Mysis* from *Diporeia* to detritus and from small zooplankton to large zooplankton, with depth.

Adult *Mysis* reliance upon a combination of benthic and planktonic foods can also be determined from Fig. 4*a*. If *Mysis* fed solely upon, for example, large plankton, its depth–$\delta^{15}N$ regression would mirror that of the large plankton line (i.e., with zero slope and lying 2.2‰ above large plankton). If adult *Mysis* fed entirely upon, for example, *Diporeia*, the *Mysis* regression would be parallel to and ~2.2‰ above the *Diporeia* regression (slope = 0.0198). Because adult *Mysis*' diet is a mixture of benthos and plankton, its slope is 0.0078, intermediate between those of plankton (0) and benthos (0.0198 for *Diporeia*). If there were no trophic fractionation of nitrogen, the *Mysis* regression line would lie between those of plankton and benthos, but the 2.2‰ fractionation lifts the line so that it (coincidentally) intersects that of *Diporeia*.

In contrast with the results for large *Mysis*, small *Mysis* relied almost entirely upon pelagic resources, especially small-fraction plankton, which accounted for ~67% of small mysid nutrition at all depths (Fig. 6*a*). Large zooplankton contributed ~30%. The total contribution of all benthic components was <5% (Fig. 6*b*). There were no distinguishable differences in the composition of small *Mysis* food sources among depths.

Adult *Mysis* have been reported to consume *Bythotrephes* in a lake in central Ontario, Canada (Nordin et al. 2008). Although this trophic linkage has not been reported in the Great Lakes, we explored its possible effects on benthic contributions to adult *Mysis* by adding *Bythotrephes* to the mixing model, to obtain a five-source solution. Finally, although oligochaetes have not been reported as a food for *Mysis*, as a fourth scenario we added oligochaetes to the model to examine a six-source solution.

Varying the sources to the mixing model had different effects in solutions for large and small mysids. Predictions of total benthic contributions to large mysids varied with the potential sources entered into the mixing model. With only three potential sources (*Diporeia* as the only benthic food, plus small and large plankton), the importance of benthic

Fig. 5. Four-source isotope mixing model estimates of (*a*) the lake-wide contributions of small- and large-fraction plankton, *Diporeia*, and detritus (as benthic nepheloid layer, BNL) to large (>1 cm) *Mysis*; (*b*) total planktonic (gray bars) and benthic (black bars) contributions.

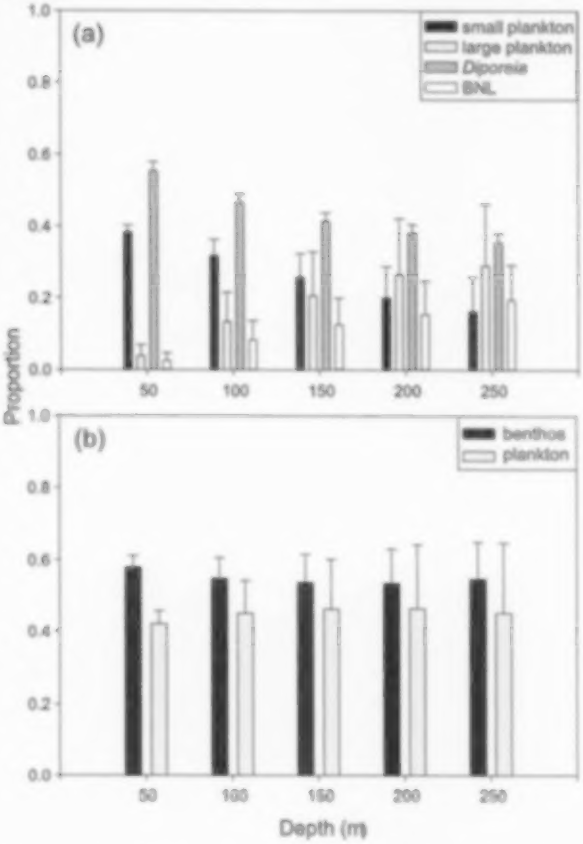
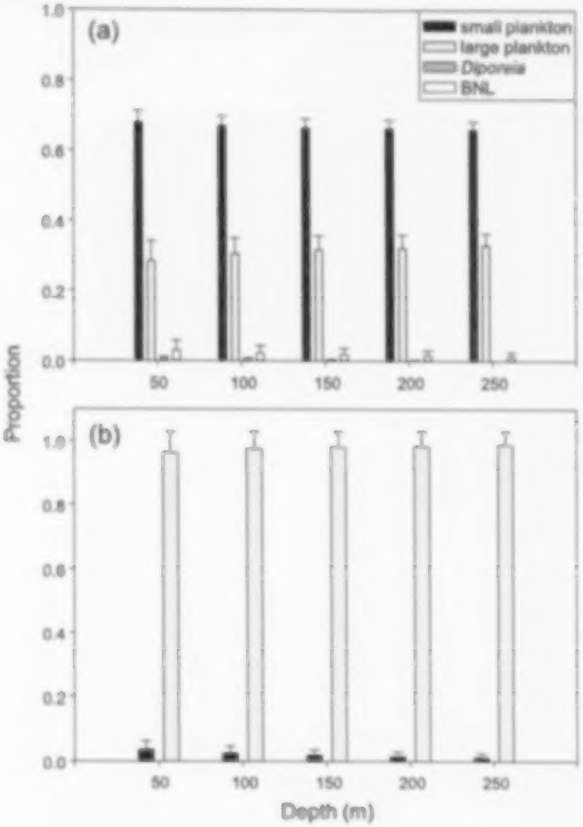


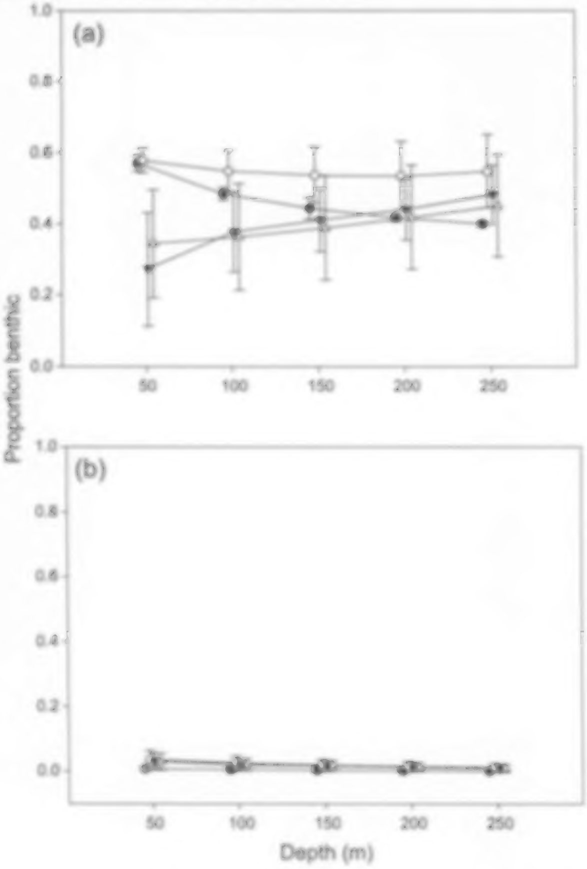
Fig. 6. Four-source isotope mixing model estimates of (*a*) the lake-wide contributions of small and large plankton, *Diporeia*, and detritus (as BNL) to small (<1 cm) *Mysis*; (*b*) total planktonic (gray) and benthic (black) contributions.



food decreased with depth from 57% to 40% (Fig. 7*a*), as predicted from declining abundance of benthos in deep zones. However, when detritus (as BNL) was added as a potential source to obtain the general four-source model, benthic nutritional sources were predicted to remain consistent (mean estimates of 54%–58%) across depths. When *Bythotrephes* was then added to the model, benthic contributions to adult *Mysis* declined because of high (22%–48% mean estimates) predicted ingestion of *Bythotrephes*. Declines in importance of *Bythotrephes* with depth appeared to drive increases in benthic contributions from 27% at 50 m to 48% at 250 m, although high associated error estimates would likely make the trend nonsignificant (Fig. 7*a*). Addition of oligochaetes to obtain a six-source solution resulted in results similar to the five-source solution. Estimates of error around the means increased with the number of potential sources. Coefficients of variation ranged from 0.02 to 0.06 for the three-source model, from 0.06 to 0.19 for the four-source general model, from 0.17 to 0.58 for the five-source model, and from 0.32 to 0.45 for the six-source model. For small mysids, model solutions were robust to variations in the number of potential sources. Total benthic contributions to small mysids under all scenarios were consistently less than 5%, with narrow error estimates (Fig. 7*b*).

Selective feeding by *Mysis* within the groups entered in the mixing model could be a possible source of variability in our analyses. For example, if *Mysis* fed selectively upon zooplankton that had isotope values that differed systematically from the average isotopic value for that size fraction, our mixing model results would contain bias. In Lake Michigan, *Mysis* was found to select cladocerans over copepods (Bowers and Vanderploeg 1982). We explored the possible consequences of *Mysis* selecting cladocerans, which would have lower $\delta^{15}N$ than omnivorous diaptomid copepods (e.g., Matthews and Mazumder 2003) that were also in the large-fraction samples. We compared the four-source (small plankton, large plankton, *Diporeia*, and BNL) solution with a scenario in which selected food (cladocerans) had very low isotopic signatures, which were as low as the mean small plankton fraction (in effect, removing the large size fraction values from the model). In the "selectivity" scenario, benthic contributions became greater than in the original solution and increased with depth. Mean (standard deviation) total contributions of benthos to large *Mysis* increased from 0.60 (0.04) at 50 m to 0.68 (0.17) at 250 m in the selectivity scenario,

Fig. 7. Model responses to differing isotope source scenarios: comparison of total benthic contributions with (*a*) large and (*b*) small *Mysis* with three sources (*Diporeia*, small and large zooplankton; closed circles), four sources (small and large zooplankton, *Diporeia*, and BNL; open circles), five sources (small and large zooplankton, *Diporeia*, BNL, and *Bythotrephes*; closed triangles), and six sources (*Diporeia*, small and large zooplankton, BNL, *Bythotrephes*, and oligochaetes; open triangles). Note the different *y*-axis scaling so that symbols in panel (*b*) can be discerned.



whereas they had been 0.58 (0.03) at 50 m and 0.55 (0.10) at 250 m in the original solution. The bias revealed under this scenario from potential effects of feeding selectivity therefore approached 13%, but were within one standard deviation of the original solution.

Discussion

We found that $\delta^{15}N$, and therefore trophic position, increased with size of *M. diluviana*. This observed ontogenetic change from planktivory to omnivory agrees with results from previous studies (Branstrator et al. 2000; Johannsson et al. 2001; Whall and Lasenby 2009). The dietary importance of plankton to small *Mysis* that we found is also consistent with reports of greater use of pelagic habitats by small mysids than by larger individuals. Smaller instars have been observed to undergo more extensive vertical migration and were found in the water column during daylight hours more so than large *Mysis* (Grossnickle and Morgan 1979; Bowers 1988; Rudstam et al. 1989). We found higher abundances of small mysids in offshore waters (>100 m), where the total planktonic biomass available throughout deep water columns is greater than that available in shallow areas. Varying the number of potential food sources in the model further illuminated the ontogenetic shifts that occur in mysid feeding. For small *Mysis*, varying the potential food sources in the model had little effect on model solutions. For large *Mysis*, changing the potential food sources in the model resulted in changes in mean estimates of benthic feeding and in the amount of variability around those means.

The different mean solutions among models derive from the combinations that best explain mysid isotope signatures given imposed restrictions in the variety of sources. In natural systems, this may be analogous to the effects of heterogeneity in prey availability or selective feeding upon them. The increasing uncertainty around model solutions as the number of sources increased was a mathematical consequence of making probabilistic predictions from many sources and few isotopes (Phillips and Gregg 2003). In another sense, however, increased uncertainty around those solutions could be viewed as there being a greater range of possible feeding behaviors when there is a greater variety of available food items.

Patterns in our abundance data confirmed previous reports showing that the biomass of benthic invertebrate food available to *Mysis* declines dramatically with depth in Lake Superior, which suggests that benthic prey should become less important in profundal zones. Mixing model results indicate that if *Diporeia* were the only (or perhaps the major) benthic food eaten by *Mysis* (i.e., the three-source model), the importance of benthos to *Mysis* would decrease with depth but would still contribute 40%. However, inclusion of detritus in the model resulted in relatively constant benthic contributions across depths. This occurred because the nutritional importance of detritus increased as the availability and use of benthic prey decreased with depth. Still, one would expect a high-quality prey item such as *Diporeia* to be preferred to detritus, and the model predicted *Diporeia* to be more important than detritus to large *Mysis* at all depths. Also, predicted contributions by *Diporeia* were greatest in the nearshore (50 m), where *Diporeia* is most abundant.

Our results indicate that on a lake-wide basis, benthic resources are important to adult *Mysis*. The overall range of modeling results constrains the estimation of mean benthic contributions to large *Mysis* within a range of 27%–58%. Under the general four-source model, benthic feeding accounted for over half (54%–58%) of adult *Mysis* nutrition at all depths. The nitrogen isotope ratios of mysid muscle tissues have been found to equilibrate with that of their food over periods of 1–2 months (Gorokhova and Hansson 1999; Johannsson et al. 2001). The nitrogen isotope ratios in our *Mysis* samples, which were taken in early September, therefore reflect feeding and assimilation during the period of high phytoplankton and zooplankton biomass in the subthermocline chlorophyll maximum that forms in the Great Lakes during summer stratification (Barbiero and Tuchman 2001, 2004*a*). This corresponds to the period of maximum mysid growth and consumption (Rudstam 1989; Johannsson 1992).

The diet of *M. diluviana* at a station in Lake Ontario was also approximately equal parts plankton and benthos, with equivalent contributions in May, a mostly planktonic diet in August, and a mostly benthic diet (especially amphipods) in September (Johannsson et al. 2001). Stable isotope analyses corroborated those results, but contributions by amphipods and phytoplankton could not be quantified (Johannsson et al. 2001). Modelling studies of the Lake Ontario pelagic food web predicted substantial predation by *Mysis* on *Diporeia* (Stewart and Sprules 2011). Also using an isotope approach, Whall and Lasenby (2009) calculated that *M. diluviana* in two British Columbia mountain lakes obtained greater than 70% of their summer nutrition from pelagic sources, regardless of mysid size class. However, as they used sediment rather than benthic invertebrates to represent benthic sources, it may be possible that benthic foods were underrepresented in their mixing model.

One might expect that benthic foods should become even more important to *Mysis* during winter months of lower plankton availability. In Lake Ontario, *M. diluviana* increased its use of planktonic resources, especially diatoms, as spring approached (Johannsson et al. 2001). Mysids in the Baltic Sea (*M. mixta* and *M. diluviana*), although primarily planktivorous during the growing season, did include benthic detritus in their diets (Rudstam et al. 1989; Viherluoto et al. 2000). Lehtiniemi et al. (2009), using a combination of dietary and isotope analyses, found that benthic foods accounted for 40%–60% of the nutrition of Baltic *M. mixta* and *M. diluviana* in the winter and that planktonic foods become more important toward spring.

Estuarine mysids similarly appear to use benthic and planktonic foods according to their availability. Although *Neomysis mercedis* is a planktivore in lakes (Murtaugh 1981), it fed on benthic copepods and detritus in the Fraser River estuary (British Columbia, Canada), which has low plankton abundance (Johnston and Lasenby 1982). In turbid European estuaries (Fockedey and Mees 1999) and a turbid Baltic coastal lagoon (Lesutienė et al. 2007) with high zooplankton abundances, mysids were primarily planktivorous but also fed on detritus. In winter, *Neomysis americana* had high ingestion rates on macrophyte detritus (Zagursky and Feller 1985). The latter authors concluded that although the detritus had low food value, detritivory may be important under conditions of low food availability. Similarly, our four-source solution predicted increased detritivory by *M. diluviana* at depths where benthic prey became less available.

Implicit in our analysis is an assumption that there was not a substantial change in the source (i.e., benthic and planktonic food) isotope signatures over the several months preceding our September sampling. Variation in source $\delta^{13}C$ over that time period should not be a major factor, as carbon isotope turnover in *Mysis* has been found to be extremely low (Johannsson et al. 2001). In contrast, $\delta^{15}N$ of *Mysis* reflects assimilation over 1–2 months (Gorokhova and Hansson 1999; Johannsson et al. 2001), and differences between our measurements of source $\delta^{15}N$ in September and source $\delta^{15}N$ during its assimilation would introduce error into our mixing calculations. It has been shown that $\delta^{15}N$ of plankton in eutrophic lakes can exhibit large (8‰–10‰) seasonal changes because of biogeochemical cycling, changes in lake N source, or changes in nutrient-limitation status (e.g., Lehmann et al. 2004). Seasonal isotope measurements of the foods available to *Mysis* in Lake Superior are not available, but we would expect relatively small shifts, as $\delta^{15}N$ seasonal variability in oligotrophic lakes is substantially less than that in eutrophic lakes (Gu 2009). In mesotrophic Lake Ontario, $\delta^{15}N$ of *Diporeia* did not change through late summer and autumn. Over that period, zooplankton $\delta^{15}N$ variation was 3‰–4‰ for epilimnetic zooplankton but 0‰–2‰ for metalimnetic and hypolimnetic taxa (*Diacyclops thomasi* and *Limnocalanus macrurus*; Johannsson et al. 2001). It is also possible that seasonal shifts in zooplankton community composition could influence our results. Populations of Lake Superior cladocerans increase in late summer (Barbiero et al. 2001), and our large-fraction plankton samples taken in early September may have had greater numbers of cladocerans than would have been present during the midsummer period represented by mysid isotope signatures. Effects on mixing model results might be expected to be similar in magnitude but the opposite of our selectivity scenario (above), with somewhat smaller benthic contributions to large *Mysis* than in the original solution.

A nitrogen trophic fractionation factor of 2.2‰ for *M. diluviana* (Johannsson et al. 2001) worked well in the mixing model, and 2.5‰ appeared to be an upper bound on the factor for *M. diluviana* in Lake Superior. However, trophic fractionation may vary among consumers and among diets. In laboratory experiments, *M. mixta* were ^{15}N-enriched by 3.6‰ relative to a diet of *Artemia* and enriched by 2.7‰ relative to a diet of detrital *Enteromorpha* (Gorokhova and Hansson 1999). It is possible, therefore, that the ontogenetic diet shifts we note in *Mysis* might result in shifts in isotope fractionation with mysid age. Similarly, if adult *Mysis* feed less upon *Diporeia* and increasingly upon detritus in deep zones, its fractionation may differ with depth. Johannsson et al. (2001) derived their parameter estimate from field samples taken in Lake Ontario, and its successful application to the Lake Superior food web suggests that it may be appropriately applied to analyze *Mysis* feeding under natural conditions in the Great Lakes.

Using samples from across Lake Superior, we calculated a trophic fractionation factor of 1.3‰ for *Bythotrephes*. Although this seems to be a low fractionation value, similarly low values have been found for other freshwater zooplankton. Cladoceran nitrogen fractionation values calculated from laboratory studies ranged as low as 1.10 (Vander Zanden and Rasmussen 2001, their appendix). Nitrogen fractionation by *Daphnia magna* was found to be inversely related to the C:N of its food and ranged from nearly 0 to ~6‰ (Adams and Sterner 2000). Using similar assumptions as in our analysis (i.e., no selective feeding by *Bythotrephes* among the bulk zooplankton collected and analyzed), we calculated comparable fractionation factors using published data from the Great Lakes (1.62‰ for Lake Michigan samples and 0.95‰ for Lake Huron samples; data in Branstrator et al. 2000) and from inland lakes in south-central Ontario, Canada (1.16‰ for Peninsula Lake and 1.67‰ for Harp Lake; data in Hatton 2008). Our factor of 1.3‰, therefore, may be a reasonable preliminary estimate of fractionation for *Bythotrephes*.

When *Bythotrephes* was added to the model, high predicted feeding on *Bythotrephes* by *Mysis* resulted in relatively low benthic contributions at 50 and 100 m, which would be unexpected given the abundance of benthic resources at those depths. In waters deeper than 30 m in Lake Superior, *Bythotrephes* constitutes less than 3% of zooplankton biomass (P.M. Yurista, unpublished data), and it is unlikely that *Mysis* feeds upon *Bythotrephes* in Lake Superior to the extent reported for a central Ontario lake that had high *Bythotrephes* abundance and low availability of alternative prey (Nordin et al. 2008). In that study, results from most invaded lakes were consistent with competition between *Mysis* and *Bythotrephes* for cladocerans, rather than a predator–prey relationship (Nordin et al. 2008). In a separate study of three *Bythotrephes*-invaded Ontario lakes, the trophic position of *Mysis* was unchanged, suggesting that *Bythotrephes* was not a major food item for *Mysis* (Foster and Sprules 2010). Because of the strong effects *Bythotrephes* has had on Great Lakes cladoceran communities (e.g., Barbiero and Tuchman 2004*b*) and *Mysis*' preference for cladoceran prey (Bowers and Vanderploeg 1982), it may currently be most appropriate to consider *Mysis* and *Bythotrephes* as competitors in most systems rather than predator and prey. Similarly, *Mysis* has not been reported to consume oligochaetes. This might be because soft-bodied oligochaetes may be difficult to identify in stomach contents. However, the dominant oligochaete in Lake Superior is *Stylodrilus heringianus* (Scharold et al. 2009), which feeds below the sediment–water interface to a depth of as much as 10 cm (Robbins et al. 1984). This probably limits its availability to *Mysis* as a prey item, and we feel that scenarios including oligochaetes (e.g., the six-source model) are not currently well-supported. We propose that the four-source model is the most likely scenario among those we have considered.

We have presented a range of diet scenarios and model solutions to explore possible benthic and pelagic nutritional contributions to *Mysis*. We then used published analyses of *Mysis*' diet to decide which scenario was best supported and addressed possible effects of selective feeding by *Mysis* on that solution. To further constrain these estimates, improved information addressing a number of assumptions would be valuable. These include seasonal measurements of the stable isotope signatures of *Mysis* and its foods, improved depth-specific dietary information, and diet-specific measurements of isotope fractionation.

The lake-wide nutritional importance of benthos to *Mysis* is meaningful to our understanding of lake processes and their responses to perturbation. Models of benthic–pelagic nutrient transport and contaminant bioaccumulation and transfer are sensitive to benthic versus pelagic food sources for biota (Fraser et al. 2005; Patwa et al. 2007) and will be improved by these and similar estimates. The ultimate effects of food web disruption in the Great Lakes may also hinge upon the role of *Mysis*. Following the invasion of Lakes Ontario, Erie, Huron, and Michigan by dreissenid mussels, populations of *Diporeia* were decimated in those lakes (Mohr and Nalepa 2005). Subsequently, the condition of lake whitefish (*Coregonus clupeaformis*), which relied strongly upon *Diporeia* as a high-quality food resource, declined in Lakes Ontario, Huron, and Michigan (Mohr and Nalepa 2005; Pothoven and Madenjian 2008). Hopes that these valuable fisheries would be sustained by a diet switch from *Diporeia* to *Mysis* (e.g., McNickle et al. 2006) were supported by some evidence of increased lake whitefish feeding upon *Mysis* (Pothoven et al. 2001; Owens and Dittman 2003). However, if *Mysis* consistently relies upon *Diporeia* and other benthos to the degree that we have found in Lake Superior, the sustained ability of *Mysis* populations to support those fisheries may be in question.

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Spatial dimension and exploitation dynamics of local fishing grounds by fishers targeting several flatfish species

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Abstract: Patch exploitation dynamics, based on individual tow data, provided new insights into the fishing behavior of mixed fisheries. Fishing grounds were determined and their geometry quantified based on the proximity of tow positions. Tows were classified as being part of either searching, sampling, or exploitation behavior based on the intertow distance. Fishers can detect patches of flatfish on a scale of ~25 nautical miles^2. Catch rate during exploitation was 24%–36% above the catch rate while searching, and decreased at a rate of 20%·day^{-1}. Once a patch was found, exploitation occurred until the catch rate dropped below a threshold level. The optimal giving-up catch rate was estimated based on the observed search time, catch rate decline, and range of fishing ground quality. The observed giving-up catch rate was 6%–11% higher than predicted by the marginal value theorem. The discrepancy between the observed and predicted patch leaving decision was consistent with the bias expected in an individual transferable quota (ITQ) management system. Our results provide a basis for interpreting vessel monitoring system (VMS) data and studying the interaction among fishers and between fishers and their resources at the appropriate time and spatial scale.

Résumé : La dynamique d'exploitation des taches, basée sur des données de tirs individuels de chalut, apporte de nouvelles perspectives sur le comportement de pêche dans les pêches mixtes. Nous avons déterminé les territoires de pêche et mesuré leur géométrie en fonction de la proximité des emplacements des tirs. D'après la distance entre les tirs, les tirs ont pu être classifiés comme faisant partie de comportements de tirs de recherche, d'échantillonnage ou d'exploitation. Les pêcheurs peuvent déceler des taches de poissons plats à une échelle de ~25 milles nautiques^2. Le taux de capture durant l'exploitation est de 24%–36% plus élevé que le taux de capture durant la recherche et décroît à un taux de 20%·jour^{-1}. Une fois la tache trouvée, l'exploitation se poursuit jusqu'à ce que le taux de capture diminue sous un seuil. Nous estimons le taux de capture optimal pour l'abandon de la tache d'après le temps de recherche observé, le déclin du taux de capture et l'étendue de la qualité du territoire de pêche. Le taux de capture d'abandon est de 6%–11% plus élevé que prédit par le théorème de valeur marginale. Cet écart entre les décisions observée et prédite de quitter la tache est compatible avec l'erreur systématique attendue dans un système de gestion avec des quotas individuels transférables (ITQ). Nos résultats fournissent une base pour interpréter les données des systèmes de surveillance des navires (VMS) et pour étudier les interactions entre les pêcheurs et entre les pêcheurs et leurs ressources aux échelles temporelles et spatiales appropriées.

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Introduction

One of the major questions fishers face is when and where to fish, and what gear to use (Hilborn 1985). Fishers are assumed to be profit maximizers, selecting the fishing time, fishing ground, and fishing gear that yields the highest revenue at the lowest cost, taking into account factors such as the risk of bad weather or management regulations (Sampson 1991; Salas and Gaertner 2004; Christensen and Raakjaer 2006).

Knowledge of the behaviour of fishers is an indispensable component of fisheries science, and is of particular relevance to understanding and predicting the responses to fisheries management measures (Degnbol and McCay 2007; Fulton et al. 2011). Management measures change the constraints under which fishing fleets operate, and trigger responses by fleets (Wilen et al. 2002), such as exit and entry decisions (Ward and Sutinen 1994; Rijnsdorp et al. 2008), fishing effort allocation, and discarding (Gillis et al. 1995*a*; Branch 2009; Poos et al. 2010*a*). In turn these responses affect the relationship between effort and fishing mortality (Marchal et al. 2002; Wilberg et al. 2010), the relationship between the catch per units effort (CPUE) and the stock biomass (Bab-

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cock and Pikitch 2000; Branch and Hilborn 2008), and influence the ecosystem impact of a fishery (Jennings and Kaiser 1998; Dinmore et al. 2003; Reiss et al. 2010). Fisheries managers and scientist have largely ignored these responses to management measures (Salas and Gaertner 2004; Fulton et al. 2011), which could jeopardize the effectiveness of any management regulations (Hilborn 1985; Salas et al. 2004; Fulton et al. 2011).

The analysis of the interaction between fishers and their resource has been hampered by the lack of experimental information and the large scale of field observations (daily or weekly data with a spatial resolution of thousand square nautical miles or more). A study of the distribution of a bottom-trawl fishery using an automated position recording system revealed that fishers showed a patchy distribution at small spatial scales and that the fishery was randomly distributed at a scale of less than 3 × 3 nautical miles (Rijnsdorp et al. 1998). The recent introduction of Vessel Monitoring Systems (VMS) by national fishery inspection services provides the high resolution data required for the study of fishing behavior. Several studies have attempted to interpret VMS data to estimate the spatial distribution of fishing effort (Witt and Godley 2007; Hintzen et al. 2010) or infer the behavior of the vessel (Mills et al. 2007; Vermard et al. 2010).

The question of where to fish (location choice) is often answered by finding the most profitable fishing grounds (Branch et al. 2005). Once a profitable fishing ground has been found, the fisher has to decide how long to stay on the ground. The decline in catch rate during exploitation affects this decision (Rijnsdorp et al. 2000*b*). An extensive body of literature on the foraging behavior of animals addresses similar questions (Stephens and Krebs 1986), and this information can be applied to fisheries science (Gillis 2003; Beecham and Engelhard 2007; Poos et al. 2010*b*). One of the key elements in foraging theory is the marginal value theorem (MVT) developed by Charnov (1976). Formulated in terms of fisheries, it states that to maximize the long term catch rate, a fisher should leave a fishing ground when the marginal catch rate at time of leaving equals the long-term average.

To understand the dynamics of fishing ground use, a method is needed to describe their location. Although it is unlikely that fishing grounds will be regularly shaped, they have generally been described using fixed grids (Gillis et al. 1993; Rijnsdorp et al. 2000*a*). An alternative approach is to use cluster analysis of fishing position recordings to obtain a more realistic description of fishing grounds (He et al. 1997; Branch et al. 2005). Once fishing grounds are delineated, their size, persistence, species composition, and exploitation dynamics can be studied.

In this paper we analyze the fishing behavior of fishers exploiting a mix of demersal flatfish species. Because demersal flatfish species cannot be detected using echosounders, fishers can only find locations of high density by trial and error. Our study focuses on the Dutch beam trawl fleet targeting sole (*Solea solea*) and plaice (*Pleuronectes platessa*) with a bycatch of other flatfish and roundfish species (Gillis et al. 2008). Landings of the beam trawl fleet are regulated by individual transferable quotas (ITQs) for sole and plaice, and national quotas for by-catch species (Daan 1997). Detailed position recordings and corresponding catch data are available for this fleet (Rijnsdorp et al. 2000*a*, 2000*b*; Gillis et al. 2008). The objectives of the paper are fourfold: (*i*) develop an objective method to delineate a fishing ground; (*ii*) study the dynamics of exploitation of the fishing grounds; (*iii*) test whether fishers' behavior conforms to the MVT; (*iv*) evaluate the importance of small scale dynamics on the interactions among fishing vessels. Insight into the dynamics of the fishing behavior is highly relevant for the analysis of VMS data. Those data are generally collected without corresponding catch information, and our study may provide insight in the behavioral modes of fisheries based only on VMS data (Mills et al. 2007; Hintzen et al. 2010; Vermard et al. 2010).

Material and methods

Data

The Dutch beam trawl fleet was composed of about 150 vessels with an engine power of more than 300hp (ca. 224 kW) in 2005. Four data sets were used in the analyses.

Data set A1 comprises high resolution data of individual tows for a sample of the fleet with information on the vessel characteristics (engine power), fishing gear, time (minute), and position (minute) of deploying and hauling the gear, as well as the catch weight (kg) of sole and plaice. The number of sampled vessels varied between 12 and 18 by year and the number of tows varied between 10 000 and 24 000 by year. In total 99 000 tows were analyzed that were collected in the period 2000–2005. For the application of the MVT to test whether fishers maximized their long term catch rate, a specific analysis of a subset of A1 was created of the seven most frequently sampled vessels, comprising between 116 and 175 fishing trips per vessel, and between 207 and 414 fishing grounds. Data set A2 comprises a subset of A1 (26 trips) for which individual skippers (8 vessels) have commented on their location choices (33 comments).

Data set B comprises position recordings available at 6-min intervals (Rijnsdorp et al. 1998) for 19 588 tows of 13 vessels collected in the period 1993–1995 (Poos and Rijnsdorp 2007*a*). These data were used to estimate the bias in surface area of fishing grounds based on tow midpoints.

Data set C comprises the European Union (EU)-logbook records of the fishing effort and landings of all Dutch vessels in the period 2000–2005 at a resolution of the fishing trip and a spatial scale of International Council for the Exploration of the Sea (ICES) rectangles of 1° longitude and 0.5° latitude (~30 nautical miles × 30 nautical miles; 1 International nautical mile = 1.85 km). This data set was used to estimate the number of other fishing vessels operating in the ICES rectangle.

Definitions

The following terms will be used throughout this paper. Although inspired by bottom-trawl fisheries, the terminology is formulated in general terms and can be applied to various types of fisheries. A fishing area is an area of a thousand square kilometres or more that encompasses several fishing grounds: smaller areas of high fish concentrations. A fishing trip denotes the period that the vessel is at sea. During a fishing trip, a vessel makes a number of tows, which involves deploying, towing, and hauling of the gear. Fishing encompasses the following activities: steaming, searching, exploitation, and floating. Steaming is the movement during which the vessel is not operating its gear. Searching and exploitation describe the activity where the gear is deployed and comprises a series of successive tows. While floating, the vessel is not fishing but is handling the gear (repairing), processing the catch, or inactive because of bad weather. The period during which a vessel remains on a fishing ground is denoted as an exploitation event. The activities defined above can easily be distinguished using logbook data of individual tows.

Determining fishing grounds

Fishing grounds were determined from the spatial concentration of individual tows in data set A1 using single linkage cluster analysis (SAS Institute Inc. 2004). This method forms disjunct clusters of tows based on geographic distance. The approach is close to the approach used by Branch et al. (2005), although we used the midpoint of each tow instead of the start and end points of the tow. Ignoring the information on start and end points makes the interpretation similar to that of VMS position recordings. The cluster analysis was carried out on the tow positions per week of individual vessels as well as all sampled vessels (fleet level). Distance between two tow midpoints was estimated according:

$$(1)\qquad d = 60 \times \sqrt{(y_1 - y_2)^2 + (x_1\cos[y_1] - x_2\cos[y_2])^2}$$

where y_1 and x_1 are the position latitude and longitude in decimal degrees of the first tow, and y_2 and x_2 are the position latitude and longitude in decimal degrees of the second tow. The distance is expressed in nautical miles and ignores the curvature of the earth's surface. The error introduced is negligible because nearest neighbor distances were less than 10 nautical miles. The weekly resolution corresponds to the typical trip duration for this fleet (Rijnsdorp et al. 1998). The analysis of single vessels yields an estimate of fishing grounds as perceived and exploited by individual vessels. The analysis of the sampled fleet yields information on the geometry of a fishing ground (catch rate and fishing effort).

The geometry of a fishing ground was estimated by comparing the surface area and major axis of fishing grounds determined with the nearest neighbor distance increasing from $k = 1$ to $k = 10$ nautical miles. The surface area was estimated using the convex-hull routine in SAS, reflecting the surface area encompassed by the polynomial connecting the peripheral positions of a cluster. This estimate will underestimate the true surface area of a fishing ground because it is based on only one position of each tow, while the length of a 2-h tow is up-to 12 nautical miles. To estimate the bias, the surface area and major axis of fishing grounds were estimated using data set B comprising tow positions recorded at 6 min intervals. The cluster analysis was performed on the midpoints of each tow, estimated from the 6-min position recordings, and the surface area of each fishing ground was determined based on the midpoints only as well as on all 6-min position recordings belonging to the clustered tows.

Statistical analysis

Three metrics of catch rate were used. Revenue was calculated as the sum of the catch weight (kg) of plaice and sole, taking account of the difference in market value between the species (revenue = 4 × kg sole + kg plaice: Rijnsdorp et al. 2000*a*). In addition the catch weight of sole or plaice were used separately. Catch rates in data set A1 were normalized to the geometric mean rate during a fishing trip ($\log_e$ (catch rate) – geometric mean) before further analysis, except for the test of the MVT (see below) when $\log_e$ transformed data of raw catch rates were used. To analyze the catch rate data, mixed effect modeling was performed with random effects for vessel (v), fishing ground (f), and interaction between fishing ground and slope in catch rate as a function of time (t). Other explanatory variables (see below) were included as fixed effects. Model selection was based on a top-down strategy with the Akaike information criterion (AIC) following Zuur et al. (2009). First we tested the random terms including all biologically plausible fixed effects (full fixed effect model) with restricted maximum likelihood (REML). Then, the fixed effects were evaluated after refitting models with maximum likelihood. Distributions of the residuals were checked by visual inspection for normality.

Behavioral analysis

Marginal value theorem

We examined the dynamics of exploitation of local fishing grounds and tested whether fishers' behavior conforms to Charnov's (1976) MVT (objectives (*ii*) and (*iii*)). The cumulative catch $c_i(t_i)$ and the corresponding catch rate $c'i(t_i)$ in a fishing ground of quality class i are a function of the residence time t_i on the fishing ground

$$(2)\qquad c_i(t) = [\exp(\alpha_i + \beta t_i) - \exp(\alpha_i)]\beta^{-1}$$

$$(3)\qquad c_i'(t) = \exp(\alpha_i + \beta t_i)$$

where α_i is the initial catch rate at the start of exploitation and β_i is the rate at which the catch rate decreases over time.

Distinguishing between the quality of n fishing grounds in terms of the density of target species, the long term mean catch rate can be written as

$$(4)\qquad R = \frac{\sum_{i=1}^{n} p_i c_i(t_i) + SC_s}{\sum_{i=1}^{n} p_i t_i + S}$$

where p_i is the probability of encountering a fishing ground of type i, t_i is the residence time, S is the time cost of finding a fishing ground, and C_s is the catch rate during searching. According to the MVT, the long-term catch is maximized when the giving up catch rate GUP ($c_i'(\widehat{t_i})$) equals a threshold value. At this threshold value, the residence times $\widehat{t_i}$ differ between fishing grounds of different quality (Charnov 1976; Stephens and Krebs 1986). The optimal GUP was estimated by solving numerically the set of equations ($i = 1$ to n) with n unknowns:

$$(5)\qquad \begin{aligned} c_1'(\widehat{t_1}) &= R(\widehat{t_1}, \widehat{t_2}, \ldots, \widehat{t_n}) \\ c_2'(\widehat{t_2}) &= R(\widehat{t_1}, \widehat{t_2}, \ldots, \widehat{t_n}) \\ &\vdots \\ c_n'(\widehat{t_n}) &= R(\widehat{t_1}, \widehat{t_2}, \ldots, \widehat{t_n}) \end{aligned}$$

The set of eq. 5 was solved using the empirical estimates of S, C_s, and β as input. The variation in the type (quality) of the fishing grounds was taken into account by generating a set of n fishing grounds with an initial catch rate α_i being normally distributed $N(\mu_\alpha,\sigma_\alpha)$ with mean μ_α and variance σ_α. The encounter probability p_i was determined by the normal probability density function and summed up to 1.

Bootstrap analysis was conducted to obtain confidence limits of the expected and observed GUP. In each bootstrap run (n = 250) a data set of 25 randomly drawn months (~100 fishing trips) was generated. For each data set, the following list of observed metrics were estimated: μ_α, σ_α, and β, the catch rate at the time of leaving the fishing ground; the mean search time and residence time. From the regression parameters and the mean search time, the MVT predicted GUP was estimated and compared to the observed GUP as well as the catch rate during searching for each bootstrap run.

Switching between target species

Because fishers are restricted by single species ITQs, we expect that they may switch between target species by avoiding species for which their ITQ is most restrictive (Branch and Hilborn 2008; Quirijns et al. 2008). Switching between target species was studied by comparing the change in $\log_e$ catch rate of sole and plaice between successive exploitation events during a fishing trip. Results were tested against the null hypothesis of random selection of fishing grounds by bootstrap analysis (1000 runs) in which successive exploitation events were drawn at random within fishing trips.

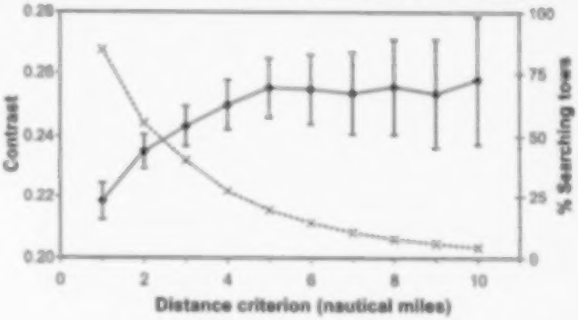
Results

Determining fishing grounds

Fishing grounds were identified from the perspective of individual fishers by cluster analysis of tow positions of individual trips based on the distance to the nearest neighbor (k). To quantify the spatial patterns at different levels of resolution, separate analyses were carried out with the nearest neighbor distance increasing from k = 1 to k = 10 nautical miles. At a distance of k = 1 nautical mile, 20% of the tows occurred in groups of 2 or more tows, while 80% of the tows remained unclustered (Fig. 1). The percentage unclustered tows quickly decreased to 40% at k = 3 and to less than 5% at k = 10 nautical miles.

The contrast in the mean normalized revenue rate between clustered and unclustered tows increased with the nearest neighbor distance up to k = 4 nautical miles (Fig. 1). For larger distances, the contrast between clustered and unclustered tows remained the same. The lowest k at which the contrast in revenue rate between clustered and unclustered tows was maximal (k = 4), provides an objective criterion to define fishing grounds and analyse fishing behavior. As an illustration, the clustering results for a single fishing trip with threshold k = 4 are shown (Fig. 2). The trip comprised 41 tows of which 33 tows were grouped in 5 clusters of ≥2 tows representing the fishing grounds (G1 to G5). Grounds G2, G4, and G5 were fished during 3–13 successive tows, but G1 and G3 were only fished during two successive tows. In the further analysis, we interpret that series of ≥3 successive tows in a cluster represent exploitation behavior, series of two successive tows represent sampling behavior and unclustered tows represent searching behavior (clusters No.1, 3, 4, 6, 7, 8, 13, 14). We also distinguish exploited grounds (G2, G4, G5) and sampled grounds (G1 and G3). Note that a ground can be visited several times as illustrated by cluster No. 11 where an exploitation phase (G4: tow 25–27) was followed by two sampling tows (tow 32–33).

Fig. 1. Contrast between the $\log_e$ normalized revenue rate (±95% confidence limits) of clustered tows and unclustered tows (♦) and the percentage of unclustered tows (×) within individual fishing trips in relation to the distance criterion (k) used in the cluster analysis.



The average normalized revenue rate during exploitation was 0.052 as compared with –0.190 during searching, a difference of 24% (Table 1). For the two individual target species, the difference was 25% for sole and 15% for plaice. The revenue rate during sampling was intermediate between the rate during exploitation and searching. The revenue rate during successive visits of the same fishing ground declined, with the exception of a few observations where a fishing ground was visited for the fifth time.

Geometry of a fishing ground

The geometry of a fishing ground was analysed by cluster analysis of the tow positions of all vessels sampled within a week. This time step corresponds to the typical weekly fishing pattern. The number of clusters distinguished is a function of k and reaches a maximum at k = 2 nautical miles (Fig. 3). At higher values, the number of clusters decreases because clusters distinguished at a lower k are merged. The clusters formed at k = 1 and k = 2 represent local hot spot of tows in the centre of a fishing ground. The decrease in the number of clusters with increasing k shows there may be more than one local hot spot within grounds identified at lower resolutions. For instance, at a resolution of k = 6 nautical miles, a total of 2933 fishing grounds were distinguished in the data set. At a higher resolution this number increased by 1743 to 4676 (k = 2). Thus in 59% (1743 out of 2933) of the fishing grounds distinguished at k = 6, there are two local aggregations of tows clustered at k = 2 nautical miles.

The average surface area of a fishing ground increased with k from 19 nautical miles^2 at k = 1 to 391 nautical miles^2 at k = 6 (Fig. 3). The surface area estimates were corrected for the bias due to the low temporal resolution of the tow midpoints. Vessels will trawl beyond the convex hull around tow midpoints during their 2-h tows. Using the highest resolution data set B, a relationship was estimated between the ratio of the surface area encompassed by the 6-min fishing positions (S_A) of the clustered tows and the surface area estimate based on tow midpoints (S_B). The relationship was

Fig. 2. Results of the cluster analysis of tow midpoints during a single fishing trip identifying fishing grounds (*a*) and modes of fishing behaviour (*b*). Series of successive tows identify fishing grounds (G1–G5). The number of successive tows distinguish between exploited grounds (black diamond, ◆) G2, G4, and G5 (≥3 successive tows) and sampled grounds (grey diamond, ◆) G1 and G3 (2 successive tows). The unclustered tows (white diamond, ◇) represent searching tows. The gridlines in panel (*b*) show spatial units for which the effort of the total fleet is recorded (ICES rectangles).

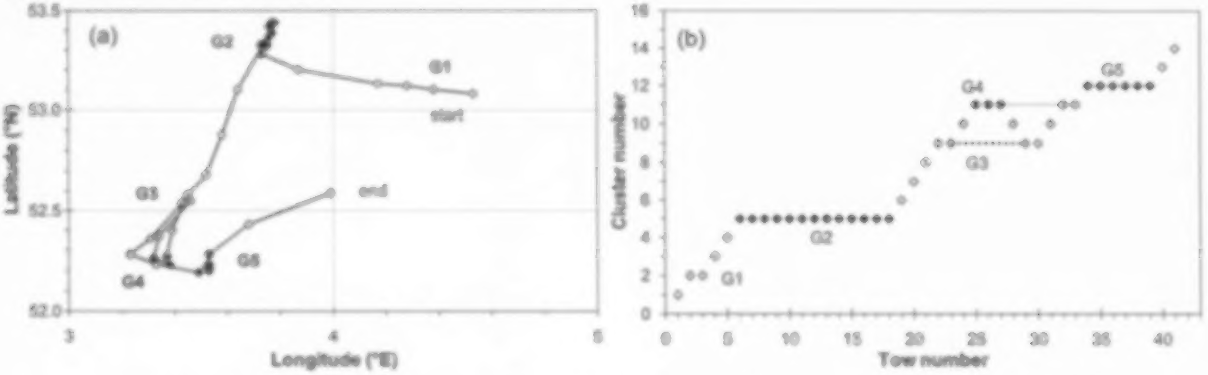
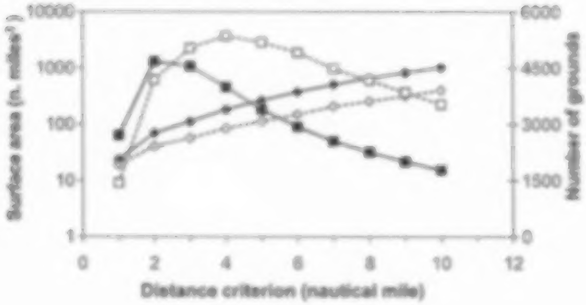


Table 1. Mean ± SD of the normalized $\log_e$ revenue (4 × sole + plaice: kg·h^{-1}) and catch rate (kg·h^{-1}) of sole and plaice for exploitation, sampling, and searching tows.

	Revenue		Sole		Plaice		
	Mean	SD	Mean	SD	Mean	SD	*n*
Exploitation tows	0.052	0.309	0.053	0.384	0.030	0.469	61 561
Sampling tows	–0.080	0.332	–0.086	0.426	–0.031	0.513	12 418
Searching tows	–0.190	0.375	–0.196	0.490	–0.124	0.548	10 971
Exploitation tows: visit No.							
1	0.0597	0.3116	0.0603	0.3875	0.0383	0.4798	49 931
2	0.0212	0.2963	0.0248	0.3727	–0.0017	0.4183	9 654
3	–0.0064	0.2979	–0.0063	0.3467	–0.0126	0.4141	1 775
4	0.0016	0.2674	0.0100	0.3211	0.0225	0.3542	173
5	0.2821	0.3003	0.2886	0.3715	0.2992	0.4212	28

Note: For the exploitation tows, results are also given for the successive revisits of a fishing ground during a single fishing trip. Results are based on cluster analysis of individual vessel data with a nearest neighbor distance criterion of $k = 4$ nautical miles. Individual vessel data (set A1).

Fig. 3. The surface area (fleet, black diamond (◆); individual vessels, white diamond (◇)) in square nautical miles (n. miles^2) and number of fishing grounds (fleet, black square (■); individual vessel, white square (□)) in relation to the distance criterion (k) used in the cluster analysis. The surface area was corrected for the bias due to the sampling interval of tow midpoints.



slightly curvilinear and was described by $\log_e S_A = 2.861 \exp(0.133 \log_e S_B)$ ($r^2 = 0.997$; $P < 0.01$; $n = 10$).

The relationship between the longest axis estimated from the high resolution fishing positions (L_A) and the tow midpoints (L_B) was estimated at $L_A = 0.9796L_B + 6.6258$ ($r^2 = 0.999$; $P < 0.01$; $n = 10$) and used to correct the tow midpoint estimate. On average, a fishing ground has an elongated shape, as reflected in the shape parameter giving the ratio between the major and minor axis (Table 2). The level of resolution slightly influenced the shape parameter which decreased from 3.6 at $k = 1$ to 2.9 at $k \geq 6$. Hence, at increasing spatial resolution the ground becomes less elongated. The elongated shape reflects that beam trawl fishers follow bathymetric contours.

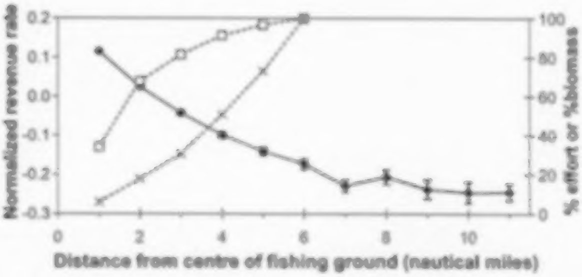
Comparison of the results of the cluster analysis with increasing resolution (*d*), allowed us to estimate how the normalized revenue rate and fishing effort change with increasing distance from the centre of a fishing ground. The mean revenue rate is highest in the centre of the fishing ground and decreases with increasing distance from the

Table 2. Surface area (nautical miles^2) and the major axis (nautical mile) of fishing grounds estimated for different levels of the nearest neighbor distance (k) based on (A) the tow midpoints and (B) the 6-min automated position recordings (APR) recorded during the clustered tows of individual vessels.

	(A) Tow midpoint		(B) 6-min APR			(C) Ratio B/A		
k	Mean surface area (n. miles^2)	Major axis (n. miles)	Mean surface area (n. miles^2)	Major axis (n. miles)	Shape (major/ minor axis)	Mean surface area	Major axis	(D) No. of observations
1	0.9	1.6	16.9	7.8	3.6	18.8	5.0	803
2	4.0	3.6	31.3	10.2	3.3	7.9	2.9	1203
3	10.8	5.8	50.3	12.4	3.1	4.7	2.1	1257
4	23.7	8.5	77.4	15.0	2.9	3.3	1.8	1181
5	45.2	11.5	113.6	18.0	2.9	2.5	1.6	1080
6	72.5	14.9	157.3	21.2	2.9	2.2	1.4	989
7	105.3	18.0	206.0	24.4	2.9	2.0	1.4	918
8	147.5	21.5	263.5	27.7	2.9	1.8	1.3	845
9	194.2	24.9	325.0	31.0	3.0	1.7	1.2	800
10	248.5	28.4	394.3	34.4	3.0	1.6	1.2	758

Note: The ratio of both surface area estimates (C) provides a conversion factor to correct for the bias in the surface area estimate based on tow midpoints. The shape parameter in B presents the ratio of the major and minor axis of the fishing ground. Individual vessel data (set B); n.miles^2, square nautical miles.

Fig. 4. Revenue rate (black diamond (◆), mean and 95% confidence interval) and cumulative percentage of fishing effort (white square, ☐) and biomass (×) within 1 nautical mile wide zones around the centre of the fishing ground. The centre of the fishing ground was defined by the cluster of tows at ≤1 nautical mile. Fleet data by week.



centre (Fig. 4). Beyond a distance of 6 nautical miles, the revenue rate reaches a stable level independent of the distance to the centre of the fishing ground. The centre of the fishing ground has a catch rate that is 36% higher than the background rate. Fishing effort is clearly concentrated within 2 nautical miles from the centre of the ground. Assuming that the revenue rate is proportional to fish density, the zone within 2 nautical miles of the centre contains only 18% of the biomass in the area within 6 nautical miles from the centre (Fig. 4).

There is a difference between the fishing grounds estimated from fleet data and those estimated from individual vessel data. Fleet data delineated fishing grounds as exploited by a group of vessels, not necessarily corresponding to grounds of individual fishers. The surface area of grounds was larger for fleet data than for individual fishers. Fleet clusters at $k = 2$ nautical miles were approximately equal in size to the cluster of tows of individual vessels at $k = 4$ nautical miles, the distance criterion at which individual vessels experienced the largest contrast in revenue rate between clustered and nonclustered tows. For fleet clusters, however, the revenue rate already fell to a level that was halfway between the peak revenue rate and the revenue rate outside the fishing ground (Table 3). This suggests that the tows of individual vessels clustered at $k = 2$ to $k = 4$ nautical miles may fall within the fishing grounds determined from fleet data using a distance criterion of $k = 2$.

Fishing behavior

The objectively defined fishing grounds and modes of behavior allowed us to describe the fishing behavior in quantitative terms (the results are summarized in Fig. 5). Most fishing trips lasted around 4 days, with only few trips lasting 9–10 days (Fig. 5*a*). The mean steaming time to the fishing ground was 5.2 h, whereas the mean steaming time to the harbour was 7.4 h (Fig. 5*b*). Vessels exploited between 1 and 9 fishing grounds during a single fishing trip, with an average of 2.7 grounds (Fig. 5*c*). The mean number of exploitation events was higher, with an average of 3.9 (range 1–10), because 42% of the fishing grounds were revisited during a single fishing trip (Fig. 5*c*). Searching time and residence time on a fishing ground showed highly skewed distributions. The mean searching time was 8.6 h (Fig. 5*d*). In 16% of the cases, a fishing ground was detected without searching, while in 50% of the cases a fishing ground was found within 6 h. Mean residence time was 15.8 h (Fig. 5*d*). In 25% of the cases, a fisher left a ground within 6 h. On the other side, the residence time on a fishing ground exceeded 11 h in 50% of the cases, and 21 h in 25% of the cases.

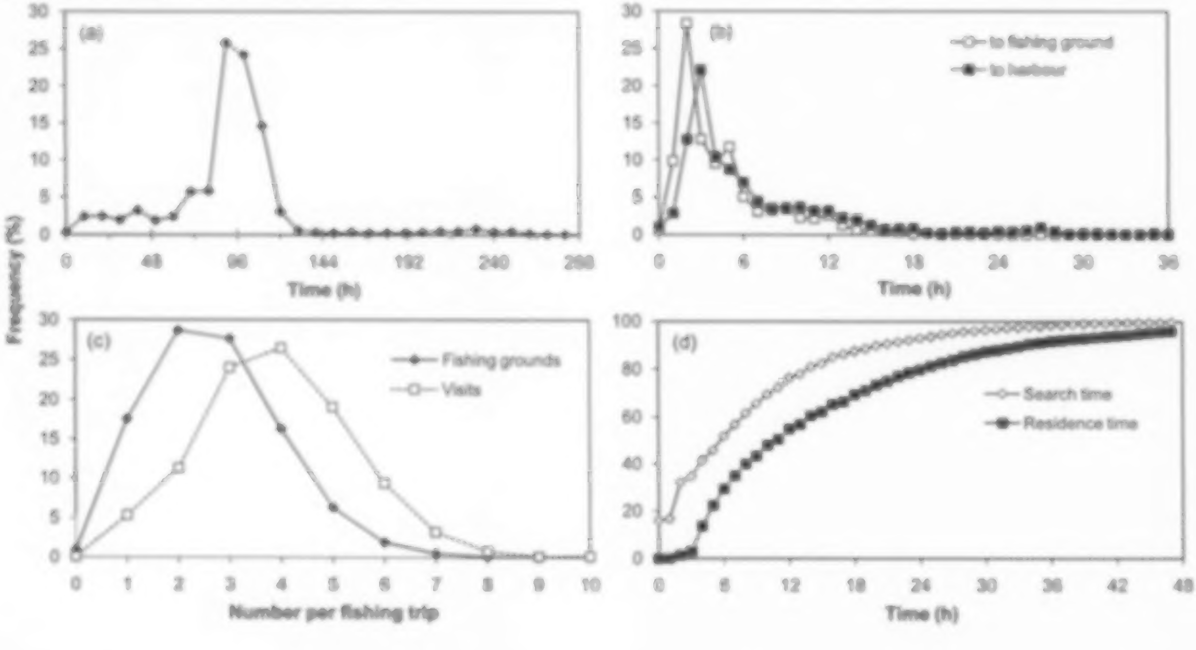
The mean revenue rate during a revisit of a ground was lower than the rate during the first visit, and decreased at subsequent visits to the same fishing ground (Table 1). Revenue rates decreased during the exploitation of a fishing ground. The start rate was well above the mean rate during the trip, whereas the GUP at the time of leaving the fishing ground was a few percent below the weekly mean, but still above the revenue rate during searching (Fig. 6). The residence time showed a clear relationship with the initial revenue rate on a fishing ground. Fishing grounds exploited for less than 10 h showed lower initial revenue rates than grounds exploited for 10 h or more. The GUP decreased slightly with residence time.

Table 3. Selection of the random effects and fixed effects of the mixed models of log$_e$ revenue rate.

Code	Model	Parms	AIC
Random effects			
1a	f	2	5607.8
1b	f×tvisit	3	5055.4
1c	v + f + f×tvisit	4	4895.2
Fixed effects: tvisit + sin(t) + cos(t) + rclass + rclass×tvisit + effort + effort×tvisit + hp + hp×tvisit			
1c	Full model	16	4801.3
2	1c – hp×tvisit	15	4800.0
3	1c – hp – hp×tvisit	14	4798.0
4	1c – effort×tvisit	15	4804.4
5	1c – effort – effort×tvisit	14	5241.7
6	1c – rclass	14	4820.1
7	1c – rclass – rclass×tvisit	12	4918.8
8	1c – rclass – rclass×tvisit – effort×tvisit	11	4922.4
9	1c – rclass×tvisit – effort×tvisit	13	4823.2
10	1c – rclass×tvisit – hp×tvisit	13	4818.6
11	1c – effort×tvisit – hp×tvisit	14	4803.5
12	1c – rclass×tvisit – effort×tvisit – hp×tvisit	12	4822.1

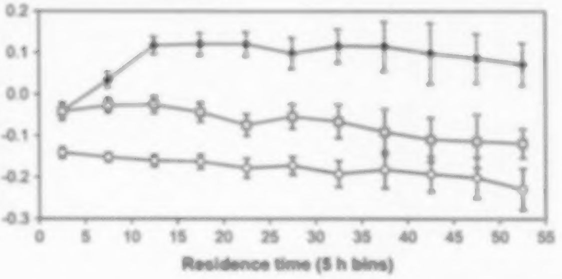
Note: Random effects are fishing ground (f), residence time (tvisit) and vessel (v). Fixed effects are residence time, time of day (t) included as a periodic function (sin(t) + cos(t)), engine power of the vessel (hp1, 1900–2200; hp2, >2200), duration of the exploitation period (rclass1, <5 h; rclass2, 5–10 h; rclass3, >10 h), total fishing effort of the Dutch fleet in the 30 × 30 square nautical miles (effort). Individual vessel data set A1 combined with effort data of total fleet from data set C.

Fig. 5. Characteristics of the fishing behavior of beam trawl fishers. (*a*) frequency distribution of trip duration (hours); (*b*) frequency distribution of steaming periods (hours) to the fishing grounds and from the fishing grounds to the harbour; (*c*) frequency distribution of the number of fishing grounds and the number of exploitation events (visits) observed during a single fishing trip; (*d*) cumulative frequency distribution of the search time and residence time (hours).



The mean rate of decline in revenue rate during exploitation, was estimated using a mixed effect model. Testing for the random effects showed that model 1c with random effects fishing grounds and the interaction between fishing ground and residence time, as well as all fixed effects, had the lowest AIC. Testing for the fixed effects revealed that model 3 had the lowest AIC (parameter estimates of the selected model are given in Table 4). The selected model showed that the revenue rate on a fishing ground was significantly influenced by the residence time, corroborating the patterns observed in Fig. 6. The rate of decline in revenue rate was highest at a residence time of 5–10 h. Revenue rates were also affected

Fig. 6. Revenue rate (mean and 95% confidence limits) at the start (black diamond, ◆) and end (grey square, ▫) of an exploitation event as well as the background catch rate during searching (white circle, ○) in relation to the residence time. Revenue rates were normalized against the geometric mean rate (GM) during each trip (hatched line). Individual vessel data A1.



by the level of fishing effort of the total fleet as recorded for the ICES rectangle in which the fishing ground was located (data from data set C). Fishing grounds in ICES rectangles that were fished intensively by the Dutch fleet showed a higher revenue rate, and showed a steeper rate of decline during exploitation. A separate analysis for the catch rate of sole and plaice showed similar results (results not shown), except in plaice, where the model tvisit + sin(t) + cos(t) + effort had the lowest AIC. The overall decline in revenue rate based on the model tvisit + sin(t) + cos(t) was estimated at $-9.5 \cdot 10^{-3}$ (SE = $4.4 \cdot 10^{-4}$) per hour, representing a decrease of 20% per day. The overall decline in catch rate was estimated at $-9.57 \cdot 10^{-3}$ (SE = $5.11 \cdot 10^{-4}$) and $-8.89 \cdot 10^{-3}$ (SE = $7.06 \cdot 10^{-4}$) per hour for sole and plaice, respectively.

A fisher must decide whether to stay put or search for a better fishing ground after each tow. To test whether beam trawl fishers maximize long term revenue by leaving when the catch rate falls below the level predicted by Charnov's MVT, the relationship between the revenue rate and residence time was estimated for seven individual vessels. For these vessels, at least 100 fishing trips were available. Pairwise comparison of the observed GUP and the GUP predicted by the MVT revealed that the difference of 6%–11% was statistically significant in 4 of the 7 vessels (Table 5), implying that vessels left their fishing grounds too early. The bootstrap analysis further revealed that the observed GUP did not differ significantly from the background revenue rate during searching, except for 2 of the 7 vessels.

To study whether fishers switch between their main prey species, the change in the catch rate of sole and plaice between successive exploitation events during a fishing trip was analyzed. This analysis showed a negative relationship between the change in catch rate of sole and plaice. The response in sole differed significantly from the change expected under the null hypothesis that fishers choose their fishing grounds in a random order, but the response in plaice did not differ significantly from a random choice of fishing grounds (model 1, Table 6). However, including other variables that may affect the relationship, such as revenue and GUP of the first exploitation event, revealed a significant negative relationship for both species. For plaice, the slope of the relationship became increasingly negative with an increase in GUP. The results thus support the conclusion that fishers switch between the two main target species during a fishing trip. Fishers leaving a fishing ground when the marginal catch rate of sole was still high were more likely to switch to plaice.

Data set A2, with the comments of fishers on their location choice, showed that 29 out of 31 comments were related to bringing the gear onboard and moving to a new fishing ground. The majority of these decisions (27) were made during a searching phase. In two instances, a fisher recorded that his decision was based on information about good fishing opportunities obtained from others. Four of the comments referred to the decision to end an exploitation phase, whereas three were related to a catch rate that was too high relative to their fishing rights. One of the decisions was related to move to a more profitable fishing ground.

Fishing patterns during a week

Beam trawl vessels typically left the harbor on a Monday morning and returned on a Thursday or Friday (Fig. 7). Only limited fishing occurred on Saturdays or Sundays. After leaving the harbor, the proportion of searching tows decreased from about 40% on a Sunday night to around 15% on Tuesdays and Wednesdays, but increased again on Thursdays and Fridays. The percentage of exploitation tows increased from almost 50% on a Sunday night to about 80% on Tuesdays, Wednesdays, and Thursdays. At the end of the week, the percentage of exploitation tows decreased. This pattern reflected the need to search for a profitable fishing ground at the beginning of the trip. The decrease at the end of the week may have been due to vessels deciding to move towards harbor while fishing, or spending some time in exploring potential new grounds for the next week. Closer inspection of the results suggested a diurnal periodicity in searching and exploitation with the percentage exploitation being highest around midnight. The percentage of searching tows on Saturdays and Sundays (23.3%) was significantly higher than on Tuesdays and Wednesdays (16.9%; *t* test of arcsin transformed data, $P < 0.01$). The percentage of tows that occurred on a fishing ground that was visited by more than one vessel was around 15% on Tuesdays, Wednesdays, and Thursdays, and followed a similar pattern as the percentage of exploitation tows. The relative pattern during the week is representative for the fleet, but the absolute level will be an underestimate, since only a sample of the fleet has been studied.

Discussion

Determination of fishing grounds

The method adopted to determine fishing grounds was based on the premise that fishers concentrate their fishing effort in areas of high fish abundance. Indeed, our results show that aggregations of fishing activity coincided with above average catch rates, corroborating the conclusions of Branch et al. (2005).

The 2 nautical mile distance criterion for the fleet data corresponds to ~0.15× the tow length (~12 nautical miles), and is close to the rule-of-thumb of 0.10–0.17 as suggested by Branch et al. (2005). The criterion for individual vessels obtained in our analysis ($k = 4$) corresponds to a cut-off point of ~0.3, suggesting that a higher cut-off point is needed when data of individual fishers are analyzed. The results of

Table 4. Parameter estimates of the selected mixed effect model (3) of $\log_e$ revenue as a function of residence time (tvisit, hours), time of day (t) included as a periodic function ((sin(t)+cos(t)), duration of the exploitation period (rclass1 = <5 h; rclass2: 5–10 h; rclass3 >10hours) and total fishing effort of the Dutch fleet in ICES rectangles of 0.5° latitude and 1° longitude (~30 × 30 square nautical miles (effort, 100 days at sea)).

Effect	Estimate	SE	df	*t*	*P*
Intercept	5.051	0.055	6	91.32	<0.001
tvisit	–0.0079	0.0007	1872	–11.67	<0.001
sin(t)	–0.0121	0.0031	10917	–3.86	<0.001
cos(t)	0.0581	0.0031	10917	18.77	<0.001
rclass 1	–0.2011	0.0240	10917	–8.37	<0.001
rclass 2	–0.1266	0.0226	10917	–5.61	<0.001
rclass 3	0				
tvisit×rclass 1	0.0010	0.0041	10917	0.25	ns
tvisit×rclass 2	–0.0096	0.0020	10917	–4.76	<0.001
tvisit×rclass 3	0				
effort	0.1159	0.0317	10917	3.65	<0.001
tvisit×effort	–0.0038	0.0016	10917	–2.36	<0.05

Note: Individual vessel data set A1 combined with effort data of total fleet from data set C.

Table 5. Results of the bootstrap (n = 250) analysis of the $\log_e$ giving-up revenue rate (GUP) of seven individual vessels.

Vessel code	(A) Difference in giving-up catch rate ($\log_e$) ($GUP_{observed} - GUP_{MVT}$)		(B) Difference in giving-up catch rate ($\log_e$) ($GUP_{observed}$ – revenue rate during searching)	
	Mean	SD	Mean	SD
1	0.075*	0.015	0.461*	0.121
2	0.117*	0.018	–0.096	0.094
3	0.088	0.052	0.103	0.092
4	0.093*	0.012	0.214*	0.096
5	0.066	0.033	–0.167	0.129
6	0.068*	0.013	0.227	0.115
7	0.105	0.057	–0.021	0.107
All	0.087*	0.038	0.103	0.228

Note: Column A presents the mean and SD of the difference for each bootstrap run between the GUP predicted by MVT and the observed GUP. Column B presents the difference in the observed GUP and the revenue rate during the searching phase. The asterisk denotes the vessels for which the difference in GUP was significant ($P < 0.05$). Individual vessel data (set A1).

our study corroborates the results of an earlier study of the beam trawl fleet where tows were classified as searching or exploitation tows based on the distance and angle between successive tows (Rijnsdorp et al. 2000*a*). The classification method was based on the behavior of the fishers changing the course of the tow by about 180° to stay on a particular ground. Both studies yielded quite similar proportions of exploitation tows per fishing trip of 20%–30%.

Whether fishing grounds need to be estimated based on fleet data or individual vessel data will depend on the research questions studied. If one is interested in the behavior of individual fishers, priority should be given to the definition based on individual data, and vice versa for the distribution of the fishing grounds of the fleet.

Fishing behavior

Our results show that trawl fishers aggregate their fishing effort on a scale of 10–50 square nautical miles. Catch-rate peaked within 2 nautical miles from the centre of the fishing ground, declined exponentially, and reached the background level at 6 nautical miles from the centre. Fishers were able to concentrate their effort in the 2 nautical mile zone of the centre of the fishing ground where more than 60% of the tows occurred. It seems surprising that fishers were able to concentrate their effort, given the 2 h tow duration and a fishing speed of about 6 nautical miles per hour. The small scale at which local fish concentrations occur implies that the efficiency with which a fisher is able to target tows in the centre of the concentrations will have a major impact on the catch rate of the fisher. This efficiency is likely an important component of the craftsmanship of fishers.

Although the catch rate in the centre of the fishing ground was on average 36% higher than the background rate, the centre accounted for only 8% of the biomass of the fish within 10 nautical miles from the centre of the fishing ground. This implies that small changes in the level of aggregation of fish may have a large impact on the catch rates of the fishery. Local concentrations are likely related to areas of high food abundance (Stelzenmüller et al. 2005; Shucksmith et al. 2006; Temming et al. 2007). Previous analyses showed that local concentrations of plaice persist for up to 2 to 3 weeks (Poos and Rijnsdorp 2007*a*), but that the catch rate on local fishing grounds recovered after the weekend with reduced fishing intensity (Rijnsdorp et al. 2000*a*). These observations are consistent with a mechanism of attraction and repulsion, where fish are attracted by the local concentrations of food and are repulsed by fishing activities of local aggregation of vessels. This mechanism may be responsible for interference competition among fishing vessels that are aggregated on local concentrations of fish (Gillis 2003; Poos and Rijnsdorp 2007*b*; Rijnsdorp et al. 2000*a*).

In contrast to an earlier analysis of data collected in the 1990s (Rijnsdorp et al. 2000*a*), the engine power of the vessels did not affect the decline in catch rate on a fishing ground. The lack of support may be due to the lack of variance in engine power in the current data set.

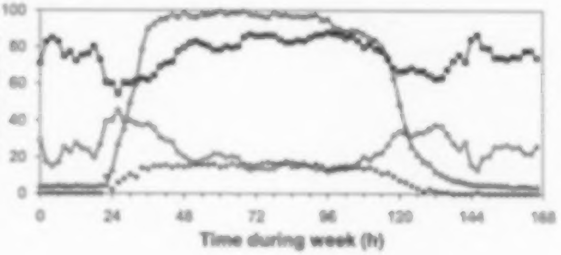
Our analysis showed that fishers were searching for fishing grounds approximately 25% of their time. This searching be-

Table 6. Parameter estimates of the generalized linear model of the change in $\log_e$ catch rate of plaice or sole (Δsole, Δplaice) on successive fishing grounds during a fishing trip (model 1) and the parameter estimates of the significant effect of revenue, giving-up rate (GUP) and the interaction between GUP and the change in catch rate (model 2).

		Observed		Bootstrap 95%CL	
Model	Explanatory variable	Mean	SE	Min	Max
Response variable: Δsole					
1	ΔPlaice	–0.184	0.032	–0.137	–0.046
2	Intercept	–2.971	0.380		
	ΔPlaice	–0.203	0.033		
	Revenue	0.357	0.075		
Response variable: Δplaice					
1	ΔSole	–0.011	0.064	–0.115	0.026
2	Intercept	–1.920	0.387		
	ΔSole	–0.048	0.063		
	Revenue	0.232	0.077		
	GUP	0.069	0.266		
	ΔSole*GUP	–1.226	0.566		

Note: The results of model 1 were tested by bootstrap analysis against the null hypothesis that fishing grounds were randomly selected.

Fig. 7. The number of observations (white triangle, Δ) and the percentage of exploitation tows (black square, ■), searching or sampling tows (white diamond, ◊) and tows on a ground shared by other vessels (black diamond, ◆) by 2-h periods during a given week. The number of tows are expressed as a percentage of the maximum number observed (n_{max} = 1711). The week starts at Sunday 0000 h. Fleet data (A1).



havior is characterized by straight line movements with relatively small changes in the fishing position, resulting in widely spaced tow positions (Rijnsdorp et al. 2000*a*). During the searching phase, fishers may decide to get their gear onboard and steam to another fishing ground, allowing them to search for local hot spots in a wider area. Comments provided by the fishers suggested that information from others is used, either via direct communication between fishers, or by using radar to infer the movement pattern of other This information use implies that the fishing efficiency will be positively affected by the number of fishing vessels operating in a certain fishing area. This inference is supported by the observation that the searching time during weekends, when most of the beam trawl vessels are in harbor, was higher than on weekdays.

Optimal foraging

The MVT predicts that (*i*) residence time increases with the quality of a fishing ground and (*ii*) the catch rate of fishing grounds of different quality will be reduced to a similar level before leaving (Charnov 1976; Stephens and Krebs 1986; Wajnberg et al. 2000). Our results were qualitatively consistent with these predictions. The residence time on fishing grounds with low initial catch rates was indeed lower than the residence time on grounds with high initial catch rates, while the differences in the GUP was only slightly different between grounds with high or low initial catch rates.

A comparison of the predicted giving up rate given the observed distribution in initial catch rates and the average decline in catch rate revealed that beam trawl fishers did not maximize their catch rate. They left their fishing grounds too early when the catch rate was on average 9% above the predicted optimal rate. This results is in contrast to many foraging studies that show that animals stay longer in a patch than predicted (Nonacs 2001), and to an experimental study on the patch leaving behavior in humans (Hutchinson et al. 2008).

The discrepancy between observed and predicted behavior may be due to beam trawl fishers violating one or more of the assumptions made in our application of the MVT: (*i*) fishers maximize their long term catch rate of plaice and sole; (*ii*) catch rate monotonically decreases in time, and (*iii*) fishers have complete knowledge on the distribution of the quality of the fishing grounds. We assumed that the catch of sole and plaice would determine the choices of our fishers. In reality, other objectives may play a role, such as minimizing daily variability in catch rate or reducing the proportion of unsuccessful fishing days. Also, other fish species contribute to the revenue. In particular species such as turbot, brill, cod, and Norwegian lobster may affect the targeting behavior of beam trawl fishers (Gillis et al. 2008). The available logbook data, however, did not consistently include catch data of other commercially important species. In addition, we ignored variations in the price of fish owing to market conditions and the size composition of the catch. Our metric of the revenue therefore is rather crude.

More important, fishers will have to deal with ITQ management constraints, which restrict the amount of sole and plaice they can land (Daan 1997). Hence a fisher will trade off the current catch rates of the ITQ species against the constraints set by the individual quota (Branch and Hilborn 2008; Quirijns et al. 2008). These management constraints will lead to the discarding of fish for which the quota are exceeded, or discarding of fish that are less valuable, to maximize the value of the landings (Gillis et al. 1995*a*, 1995*b*; Poos et al. 2010*a*). The ITQ management thus constrains a fisher to maximize its long term catch rate as he may have to leave a profitable fishing ground when the marginal catch rate is still high, to search for an alternative profitable fishing ground with a different catch composition that better matches the remaining fishing rights. We indeed found that fishers tend to switch between the two main target species during a fishing trip, as well as tend to leave a fishing ground when the marginal catch rate of sole was high to switch to another fishing ground with less sole and more plaice. Poos et al. (2010*a*) showed that in 2003–2004, fishers experienced restrictive sole quota affecting their spatial fishing patterns as well as high-grading decisions.

Second, our formulation of the MVT assumed that the $\log_e$ (catch rate) monotonically decreased with the residence time on a ground. A detailed analysis of the residuals of our model showed that for fishing grounds with residence times of more than 10 h ($\geq$5 tows), the catch rate did not decline monotonically in time, but remained stable or even increased slightly during the first 10 h of fishing (see also Fig. 6 in Rijnsdorp et al. 2000*a*). This nonlinear trend may reflect the necessity of a beam trawl fisher to determine the area of the highest catch rate by trial and error from the spatial delineation of the highest catch rates. Hence, the rate at which the catch rate decreased may be underestimated, leading to an overestimate of the optimal residence time.

Third, fishers will not have perfect knowledge about the distribution of high and low quality grounds. Hence, they have to sample the environment continuously to update their imperfect mental map of the resource distribution. One may wonder how well a fisher is able to estimate the rate of decline in catch rate at a fishing ground when the delineation of the fishing ground is unknown and needs to be estimated simultaneously. Hutchinson et al. (2008) tested patch-leaving decisions in humans using a computer game and showed that subjects responded to the catch rate as well as the time spent in the current fishing ground. Self-reports supported this order of importance. The expected mean catch rate in a fishing area, therefore, might serve as a rule of thumb to decide when to leave a fishing ground.

The test of applicability of the MVT showed that the observations were only qualitatively in correspondence with the predictions about the maximization of the long-term catch rate. The discrepancy between the predicted and observed GUP may be partly explained by the ITQ management constraints, which will force the fisher to match their catch composition with the composition of the remaining landing rights. The observation that high GUPs were positively related to a change in the species composition in the subsequent fishing ground lends support for the usefulness of the MVT in understanding the dynamics of fisheries. This inference is supported by the information obtained from the fishers providing comments on their location choices and reporting that they left a profitable fishing ground because of too high catch rates of one of the ITQ species.

We have shown that it is possible to objectively determine the behavioral mode of fishers based on the locations of tow midpoints and catch rates. The method creates the possibility of studying the interaction processes among fishers and between fishers and their resources at the appropriate temporal and spatial scale. It also allows us to study how location choice is affected by the experiences during previous trips, and how information exchange may affect location choice. Our results provide a basis for interpreting VMS data from beam trawl fisheries in terms of fishing behavior. The behavior of the beam trawl fleet seems typical for trawl fisheries suggesting that this method may be more widely applicable in trawl fisheries. As such it offers an alternative approach to the Hidden Markov Chain method developed by Vermard et al. (2010). The application of the MVT showed that the behavioral ecological theory developed on animal foraging, can successfully applied to fisheries systems. The departure of fish harvesters from fishing grounds prior to the predictions of the MVT may reflect the impact of management constraints on fishing activities. Alternatively, it could reflect inaccuracies in the representation of catch value which ignored the contribution of other species and variations in price among size classes and species.

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A spatial model for fishery age-selection at the population level

David B. Sampson and Robert D. Scott

Abstract: Different age classes do not generally experience the same rates of fishing mortality. The processes resulting in age- (or length-) selection operate at several scales. At the broadest scale, population-selection measures the age-specific probability of capture, while at the finest scale contact-selection describes the vulnerability of fish that encounter the fishing gear. Population-selectivity is the process most relevant to fish population dynamics and stock assessment, but it has received far less attention than processes operating at gear-specific scales. Despite wide recognition of the diverse shapes possible for population-selectivity, the processes determining these shapes are poorly understood. This paper develops a reasonably simple model of population-selectivity from a set of survival equations, coupled to allow movement between subpopulations, and explores the conditions necessary to produce different shaped population-selection curves. Important factors influencing the population-selectivity model are the gear-specific selection characteristics of the fleets, their effort levels relative to one another, the spatial distribution of fishing mortality, and the movement of fish between subpopulations. The model can generate quite complicated curves and has surprising properties. For example, under a wide variety of conditions, even though the same asymptotic gear-selectivity applies in all subpopulations, the overall population-selectivity will be dome-shaped unless fishing mortality is uniform across all subpopulations.

Résumé : Les différentes classes d'âge ne subissent généralement pas les mêmes taux de mortalité due à la pêche. Les processus qui expliquent la sélection en fonction de l'âge (ou de la taille) agissent à plusieurs échelles. À l'échelle la plus large, la sélection de la population décrit la probabilité de capture spécifique à l'âge et, à l'échelle la plus fine, elle représente la vulnérabilité des poissons à la rencontre des engins de pêche. La sélectivité de la population est le processus le plus pertinent pour la dynamique de population et l'évaluation des stocks de poissons, mais elle a été beaucoup moins étudiée que les processus qui agissent aux échelles spécifiques aux engins de pêche. Bien que l'on reconnaisse qu'il existe diverses formes de courbes possibles de sélectivité de la population, les processus qui déterminent ces formes restent mal compris. Notre travail met au point un modèle relativement simple de sélectivité de la population à partir d'un ensemble d'équations de survie, couplées de manière à permettre des déplacements entre les sous-populations, et explore les conditions nécessaires pour la production des différentes formes de courbes de sélection de la population. Les facteurs importants qui influencent le modèle de sélectivité de la population sont les caractéristiques spécifiques de sélection des flottes de pêche en fonction des engins, les niveaux d'effort de pêche des flottes les unes par rapport aux autres, la répartition spatiale de la mortalité due à la pêche et les déplacements des poissons entre les sous-populations. Le modèle peut produire des courbes assez complexes et il possède des propriétés plutôt étonnantes. Par exemple, sous une large variété de conditions et bien que la même courbe asymptotique de sélectivité de l'engin de pêche s'applique à toutes les sous-populations, la sélectivité globale de la population aura une courbe en forme de dôme à moins que la mortalité due à la pêche ne soit uniforme dans toutes les sous-populations.

[Traduit par la Rédaction]

Introduction

A feature common to most types of fishing gear is that they are not uniformly effective at capturing the full spectrum of length classes of fish present in a population. Most fishing processes deliberately try to catch big fish that produce larger per-recruit yields and command higher prices. Small fish are under-represented in the catches either because these fish are able to escape from the gear or because the gear is deployed in areas where small fish are less prevalent. This phenomenon of fishing effectiveness varying with the size of the fish is generally described as selection or selectivity (Bever-

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ton and Holt 1957; Quinn and Deriso 1999). Because fish generally increase in length as they age, the processes that result in selection by size also produce selection by age. The term "selective fishing" is also used to describe the ability of fishing operations to target certain fish species and avoid the incidental bycatch of species that have special legal status (e.g., trawl-caught halibut in Alaska; Rose and Gauvin 2000) or that require protection from fishing because of low levels of abundance (e.g., Hannah et al. 2005; Madsen et al. 2006). The study here focuses on the first form of selectivity, namely for different ages (or sizes) from a single target species.

Millar and Fryer (1999) distinguish between three types of length-selection curves. The population-selection curve measures the probability that a fish of a given length in the population is captured; the available-selection curve measures the probability that a fish of a given length is captured when it is available to the gear (e.g., in the path of a trawl); and the contact-selection curve, which they also describe as the retention curve, measures the probability that a fish of a given length is captured when it comes in contact with the gear. The three types of curves differ with regard to the spatial scales over which they operate, with population-selection acting on the broadest scale and contact-selection acting at the finest scale. The population-selection process is the one most relevant to fish population dynamics and stock assessment (Nedreaas et al. 1996; Sun et al. 2002).

Most of the myriad of published studies on selectivity have focused on measuring contact-selection curves (e.g., Pope et al. 1975; Wileman et al. 1996) or understanding factors that influence this relationship (e.g., Dahm et al. 2002). There have been a few published studies that have attempted to measure and understand factors influencing available-selection curves (e.g., Engås and Godø 1986; Somerton et al. 1999). The focus of the current study is the population-selection curve, which measures the size- or age-dependent fishing mortality experienced by a fish population. Our analysis does not distinguish between available-selection and contact-selection. Instead we make a distinction between population-selection versus gear-selection, with the second form encompassing both available-selection and contact-selection. Fundamental to our model is the division of the fish population into subpopulations that occupy distinct spatial regions. Gear-selection operates at the level of these subpopulations. Also, our analysis focuses on age-based selection and ignores the added complexity that is required to account for variability in length at age (e.g., Quinn and Deriso 1999; Punt et al. 2002).

Materials and methods

In an age-structured model for fish population dynamics, when the instantaneous rate of fishing mortality (F) during a year (or other suitable time step) is not the same for all age classes, so that fishing mortality is age-dependent, the selection (or selectivity) coefficients measure the relationship between age a and F_a, after standardization to account for year-to-year changes in the overall rate of fishing. The set of points (a, F_a) is often represented by a smooth curve passing through all the points. If the F_a values are uniform across all age classes, then the selection curve is a horizontal line and we can state that there is no selectivity. If the selection coefficients increase with age to a plateau, we can describe the selection curve as being asymptotic. If the selection coefficients increase to a maximum and then decline, we can describe the selection curve as being domed or dome-shaped. Although this concept of a selection curve implies that selectivity is a continuous function of age, selection curves are commonly used with data that have been discretized into age or length classes.

The mathematical definition of selectivity differs across regions. On the Pacific side of North America the F_a values within a year are usually standardized into selection coefficients by dividing each F_a value by the maximum value observed for any age class in that year (e.g., Deriso et al. 1985). In Europe and on the Atlantic side of North America the F_a values are usually standardized by dividing by the average (called $\overline{F}$) of the F_a values observed over a defined range of age classes (e.g., Darby and Flatman 1994). In stock assessment and fishery population dynamics models, the individual F_a values for a given year (y) are recovered by multiplying the selection coefficient with that year's maximum F_a or $\overline{F}$ value, as in

$$F_{a,y} = \max(F_{a,y})S_a \quad \text{or} \quad F_{a,y} = \overline{F}_y S_a$$

If selectivity in the model varies from year to year, then the selection coefficients (S_a) would include an index for the year ($S_{a,y}$). These selection coefficients define the population-selection curve.

Simplified spatial model for population age structure

To explore the role of the population-selection curve in fish population dynamics, consider the population to be partitioned into distinct subpopulations occupying discrete spatial regions (indexed by r), with some limited exchange of fish between the regions. The fish within each region all suffer the same instantaneous rate of natural mortality (M for all ages), but they potentially experience different instantaneous rates of age-specific fishing mortality ($F_{a,r} = F_r s_a$). In this formulation the gear-selection curve (s_a) is the same across all regions, but the fish in each region suffer a (potentially) different absolute level of fishing mortality. We describe the s_a values, denoted by a lower case S, as the gear-selection curve to distinguish them from the age-specific relative F values that are derived by combining the fish in the separate regions. The population-selection values (S_a, denoted by an upper case S) are a composite, weighted average of the F_a values operating in each region. The population-selection curve will be the same as the gear-selection curve only under special circumstances (below).

If the population is exploited by several types of fishing gear that differ in their gear-selection characteristics, then each gear type would have its own selection curve ($s_{a,\text{gear}}$), and we would partition the age-specific, instantaneous rates of fishing mortality accordingly. For now we assume that all gear types have the same gear-selection curve.

To keep the notation and mathematics relatively simple, we use the standard exponential decay equation to represent the mortality processes operating within each region during a year (or other unit time step). At the end of each year, the fish mix instantaneously among the regions. Further, we consider only the equilibrium situation in which recruitment to each region and the rates of fishing mortality within each region are constant from year to year. The assumption of constant recruitment could be relaxed, but in this case the equations below apply to the age classes in a single year class, and the variable for abundance should have a subscript for year as well as age and region. The equilibrium assumption avoids this notational complication.

For each age class a, the number of living fish at the start of each year within region $r = i$ is given by

$$(1)\qquad N_{a,i} = N_{a-1,i}\exp(-M - F_i s_{a-1})(1 - \sum_{i\neq j} P_{j,i}) + \sum_{i\neq j} N_{a-1,j}\exp(-M - F_j s_{a-1}) P_{i,j}$$

The coefficient $P_{j,i}$ denotes the proportion of fish that move into region j from region i. The first term in the right-hand side of eq. 1 represents the individuals in the focal region i at the start of the year that survive and remain in the region; the second term represents the individuals that move into the region from the other regions.

Mortality in this formulation is treated as a continuous process, but movement occurs abruptly (and unrealistically) at the end of each year. The equation can be viewed as an approximation to a differential equation system in which there is continuous movement of fish among regions. When the mixing rates are high and nondirectional, one can ignore the regional differences and treat the population as occupying a single region. Equations similar to eq. 1 have been used to represent spatial fish population dynamics in stock assessment models (Hampton and Fournier 2001), in models of no-take marine reserves (Apostolaki et al. 2002), and in the operating models for management strategy evaluations (e.g., Punt et al. 2002; Pelletier et al. 2009).

Equation for population-selectivity

At the population level, the number of age-a fish alive at the start of each year is given by the age-specific abundances summed over all the regions.

$$(2)\qquad N_a = \sum_r N_{a,r}$$

The population-selection coefficients are proportional to the age-specific fishing mortality coefficients for the population, which, because of the equilibrium condition, can be obtained from the ratios of successive N_a values.

$$(3)\qquad F_a = -\ln\left(\frac{N_{a+1}}{N_a}\right) - M$$

$$S_a = \frac{F_a}{\max(F_a)}$$

The divisor in the equation for S_a is shown here as the maximum F_a value, but we could instead use the average F_a value ($\overline{F}$), with the average taken over some suitable age range.

By substituting the right-hand side of eq. 1 into eqs. 2 and 3, we can derive a messy equation that relates population-selectivity with gear-selectivity.

$$(4)\qquad S_a = \frac{-\ln\left\{\dfrac{\sum_i [N_{a,i}\exp(-Z_{a,i})(1 - \sum_{i\neq j} P_{j,i}) + \sum_{i\neq j} N_{a,j}\exp(-Z_{a,i}) P_{i,j}]}{\sum_i [N_{a-1,i}\exp(-Z_{a-1,i})(1 - \sum_{i\neq j} P_{j,i}) + \sum_{i\neq j} N_{a-1,j}\exp(-Z_{a-1,j}) P_{i,j}]}\right\} - M}{\max(F_a)}$$

Here the gear-selection coefficients (s_a) are embedded in the age- and region-specific total mortality coefficients, $Z_{a,r} = M + F_r s_a$.

The above model for population-selectivity has no provision for a plus-group, which is an accumulator class for all the ages greater than some reference age. Stock assessment models commonly use a plus-group to reduce the number of age categories that must be accounted for. This simplification assumes that the vital rates for these older age classes are sufficiently similar that they can be treated in the aggregate with inconsequential loss of accuracy. The underlying mathematical equation for plus-group abundance follows from

$$N_{a+} = \sum_{i=a}^{\infty} N_i = N_a + N_a\theta + N_a\theta^2 + N_a\theta^3 + \ldots = \frac{N_a}{1-\theta}$$

where θ is the annual survival fraction, assumed constant for all ages equal to a or greater. In the model for population-selectivity, one cannot apply a similar approach unless one assumes that there is no movement of fish among the different regions. When there is movement of fish among regions, the abundance for a given region at the start of an age class depends not only on the survivors from that region but also on the survivors from other regions.

The population-level fishing mortality and selection coefficients satisfy the catch equation for the population.

$$C_a = N_a \frac{FS_a}{Z_a}[1 - \exp(-Z_a)]$$

where $Z_a = M + FS_a$. Similarly, for each region the region-level fishing mortality and selection coefficients satisfy a region-level catch equation.

$$C_{a,r} = N_{a,r} \frac{F_r s_a}{Z_{a,r}}[1 - \exp(-Z_{a,r})]$$

where $Z_{a,r} = M + F_r s_a$. These equations are just extensions to the calculation of effective fishing mortality described in Beverton and Holt (1957).

From eq. 4 it is difficult to discern the behavior of the population-selection curve because each S_a value is the logarithm of the ratio of two sums of exponentials. However, for a certain special case this defining equation can be greatly simplified. Before considering this case, we first determine the general conditions required to produce a decreasing (or increasing or constant) sequence of population-selection coefficients.

Conditions for dome-shaped population-selection curves

The population-selection coefficients are just scaled F_a values and will decrease (or increase) with age if the F_a values for adjacent age classes are decreasing (or increasing). Population-selectivity is decreasing if and only if the following conditions are satisfied:

$$(5)\qquad F_{a+1} = -\ln\left(\frac{N_{a+2}}{N_{a+1}}\right) - M < F_a = -\ln\left(\frac{N_{a+1}}{N_a}\right) - M$$

$$N_{a+2}N_a > (N_{a+1})^2$$

Assuming that selectivity is smallest for the youngest age classes, if inequality condition 5 is satisfied for at least one age class, then the population-selection curve will be dome-shaped or will have a local maximum at an intermediate age. If condition 5 is not satisfied for any age class, then the population-selection curve will be strictly increasing, or increasing and then horizontal, or just horizontal. The population-selection coefficients will be the same for adjacent age classes (a, a+1) if and only if $N_{a+2}N_a = (N_{a+1})^2$.

Direct substitution of the general equations for N_a, N_{a+1}, and N_{a+2} into condition 5 produces a very untidy expression that appears intractable, but useful results can be obtained for the simpler problem in which there is no movement of fish between the regions ($P_{ji} = 0$ for all regions j and i) and the gear-selection coefficients are the same for the three adjacent age classes ($s_a = s_{a+1} = s_{a+2} = s$). In this special case, it is shown in Appendix A that condition 5 reduces to the following:

$$(6)\qquad \sum_{i \neq j} N_{a,i}N_{a,j}\exp(-2M)[\exp(-F_i s) - \exp(-F_j s)]^2 > 0$$

Because M is always nonnegative, the initial exponential term in eq. 6 is positive for all combinations of regions, and the condition will be satisfied except when the final squared term is zero, which occurs if $F_i = F_j$ for all i and j, or in the limit as the F_i go to zero. That is, even though the gear-selection curve is flat for some set of age classes, the population-selection curve for those same age classes will also be flat only if the same rate of fishing mortality is applied in all regions or if the rates of fishing mortality are vanishingly small. Otherwise the population-selection curve for this set of age classes will be declining; the population-selection curve will be dome-shaped. Also, from condition 6 it is evident that the degree of difference among the regional F values controls how much the population-selection curve departs from flat selection. The greater the differences among the F values, the more pronounced the domed shape.

Composite gear-selectivity from multiple gear types operating in the same region

When different types of fishing gear, with differing selectivity characteristics, operate together in some region r, then the overall age-specific fishing mortality for the fish in that region will be the summation of the age-specific fishing mortality rates produced by each gear type.

$$(7)\qquad F_{a,r} = F_{r,\text{gear.1}} \cdot s_{a,\text{gear.1}} + F_{r,\text{gear.2}} \cdot s_{a,\text{gear.2}} + \dots$$

These composite $F_{a,r}$ values substitute for the $F_r s_a$ terms in eq. 1. The composite gear-selection coefficients for region r are obtained from successive values of $N_{a,r}$.

$$(8)\qquad F_{a,r} = -\ln\left(\frac{N_{a+1,r}}{N_{a,r}}\right) - M$$

$$s_{a,r} = \frac{F_{a,r}}{\max(F_{a,r})}$$

The gear-selection curve for the region is a weighted average of the different individual gear-selection curves and is directly influenced by the relative amounts of fishing mortality produced by the different gear types.

Exploring the shape of population-selectivity curves

To explore the possible shapes of population-selection curves we developed a spreadsheet model[1] that implements eq. 4 for three regions, 15 age classes, M = 0.2 year^{-1}, 3000 recruits annually, and logistic curves for gear-selectivity. We considered a series of four scenarios in which all regions have the same gear-selection curve but have different conditions for fish movements, the rate of fishing mortality, and the number of recruits.

In scenario 1, the simplest case, there is no movement of fish between regions and the initial recruitment is uniform across the regions. This is an idealized situation that might be realistic for some sessile organisms, but probably it is unrealistic for most fish species. It corresponds to the circumstances that produced condition 6, which indicated that selectivity is domed unless the rates of fishing mortality in the regions are all equal or are vanishingly small. We used the spreadsheet model to generate population-selectivity curves for situations where the rate of fishing mortality in region 1 is twice the level in region 2, which is twice the level in region 3. In case A the F values are (0.4, 0.2, 0.1); in case B they are (0.08, 0.04, 0.02), smaller by a factor of five.

Scenario 2 is similar to scenario 1 in that recruitment is spread uniformly, but there is symmetric dispersion of fish between the regions at a rate of 5%·year^{-1}. We considered two cases that differ in the regional fishing rates. In case A the F values are (0.4, 0.2, 0.1), as in case A of scenario 1; in case B they are (0.4, 0.2, 0.0), to mimic the effect of a no-take reserve in region 3.

Scenario 3 uses the same set of parameters as case A of scenario 2, but the regional distribution of recruits is no longer uniform. Instead they are distributed to regions as (1500, 1000, 500). Again, we considered two cases that differ in the regional fishing rates. In case A the F values are (0.4, 0.2, 0.1), as in case A of scenarios 1 and 2; in case B they are reversed (0.1, 0.2, 0.4).

In scenario 4, which is the most complex one that we considered, all the recruits begin in region 1 and gradually disperse (5%·year^{-1}), first into region 2 and then into region 3.

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[1] Supplementary data are available with the article through the journal Web site (http://nrcresearchpress.com/cjfas).

This form of slow directional movement results in differences in the regional age distributions, with higher than average numbers of young fish in region 1 and higher than average numbers of old fish in region 3. It is a simple modeling trick for mimicking ontogenetic movement of the fish, for example from nearshore nursery areas to different grounds where adults are found. Again, we considered two cases that differed in the regional fishing rates. In case A the *F* values are (0.4, 0.2, 0.1), as in case A of scenarios 1, 2, and 3; in case B they are reversed (0.1, 0.2, 0.4).

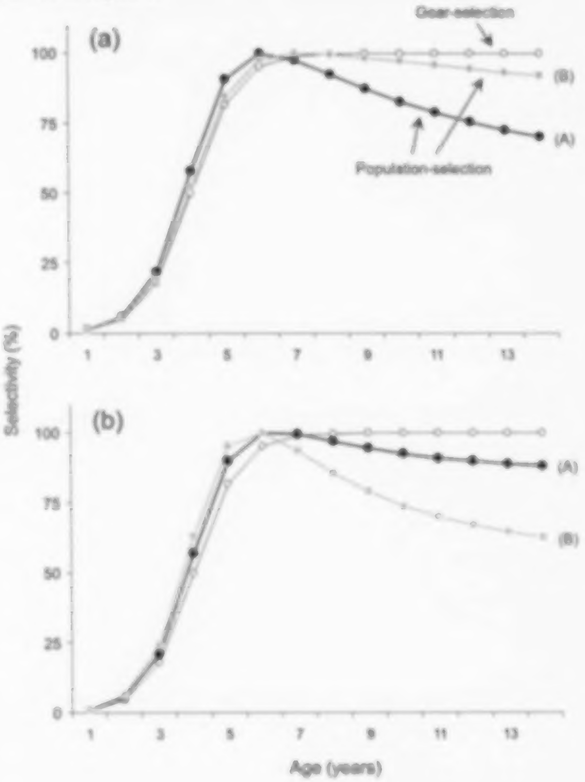
In addition to the four scenarios described above, in which there was a single asymptotic gear-selection curve, we also explored the possible shapes of population-selection when there are two distinct gear-selection curves. For scenario 5 the model was configured identically to case A of scenario 2 except that the gear-selection curves for regions 2 and 3 were shifted to the right by four age units. This mimics conditions in a fishery for which there is spatial segregation of two distinct gear types (e.g., small-mesh versus large-mesh trawls). Further, we adapted the spreadsheet model to explore composite gear-selection curves based on modifications to eq. 4 that incorporated eqs. 7 and 8. Scenario 6 was configured identically to scenario 5 except that region 2 had a composite gear-selection curve that was a 50:50 mixture of the two asymptotic gear-selection curves that were applied separately in regions 1 and 3, thus mimicking a situation where there is partial spatial segregation of two gear types.

Results

The model for population-selectivity has four main types of parameters: the set of regional fishing mortality coefficients, the set of spatial movement coefficients, the spatial distribution of the recruits, and the curve (or curves) for gear-selection. With the spreadsheet version of the model, we explored the influence of these parameters. Scenario 1 examined the effect of changing the scale of the fishing mortality coefficients (Fig. 1*a*). The fivefold reduction in the *F* values caused a considerable reduction in the magnitude of the domed shape. Further reductions in the *F* values (not shown in a figure) caused the population-selection curve to become increasingly similar to the underlying gear-selection curve. When the regional *F* values were all equal (to any positive value), then the population-selection curve was identical to the common asymptotic gear-selection curve, as predicted by condition 6.

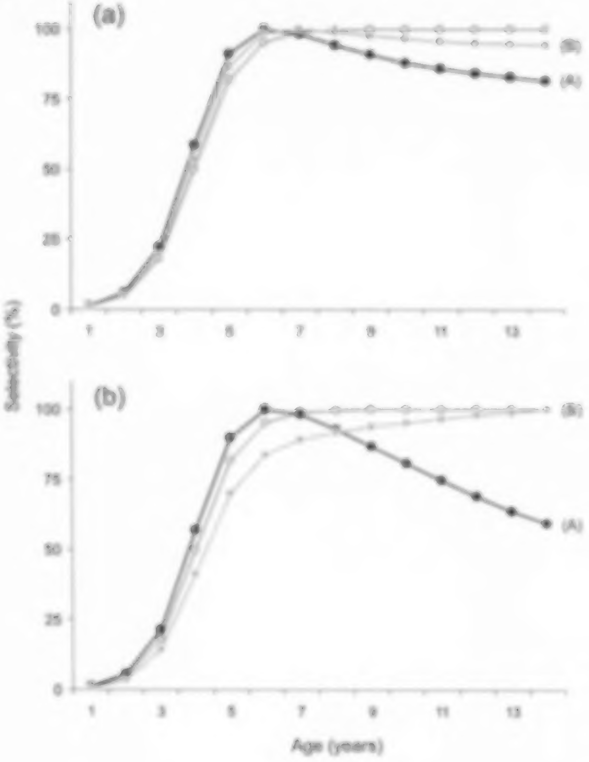
Scenario 2 explored the effect of eliminating fishing in a single region (Fig. 1*b*) and, when compared with case A of Fig. 1*a*, the effect of nondirectional spatial dispersion. When there was no fishing in region 3, the domed shape of the population-selection curve became more exaggerated (Fig. 1*b*, line B). If fishing was eliminated from either of the other regions (not shown in a figure), the population-selection curves had a similar shape but with a less pronounced dome. Regarding the effect of dispersion, the population-selection curve was less pronounced when there was dispersion (Fig. 1*b*, line A) than when there was no dispersion (Fig. 1*a*, line A). As with scenario 1, the population-selection curve was identical to the gear-selection curve if $F_1 = F_2 = F_3$. This result is consistent with condition 6 even though the derivation of that condition was based on the assumption of no fish movements between regions.

Fig. 1. Population-selection curves generated by a three-region spreadsheet model with differing instantaneous rates of fishing mortality in each region. All regions have the same asymptotic gear-selection curve, shown by the thin line with small open circles. In the upper panel (*a*), there is no movement of fish between regions and fish recruit equally to each region. In case A, shown by the thick, black line with larger solid circles, the regional rates of fishing mortality are (0.4, 0.2, 0.1); in case B, shown by the grey line with grey solid circles, they are (0.08, 0.04, 0.02), smaller than in case A by a factor of five. In the lower panel (*b*), there is symmetric dispersion of fish between regions at a rate of 5%·year^{-1}. In case A, shown by the thick, black line with larger solid circles, the regional rates of fishing mortality are (0.4, 0.2, 0.1), the same as in case A in the upper panel. In case B, shown by the grey line with grey solid circles, the *F* values are (0.4, 0.2, 0.0), to mimic the effect of a no-take reserve in region 3.



Scenario 3 explored the effect of the spatial distribution of fishing relative to the spatial distribution of the recruits (Fig. 2*a*). Population-selectivity had the strongest domed shape in case A in which the rates of fishing were almost proportional to the recruit values. Relative to case A of Fig. 1*b*, in which the recruits were evenly distributed, the population-selectivity curve had a more pronounced dome (Fig. 2*a*, line A). As with scenarios 1 and 2, the population-selection curve was identical to the gear-selection curve if $F_1 = F_2 = F_3$.

Fig. 2. Population-selection curves generated from nonuniform regional distribution of the recruits, but otherwise with similar conditions as in Fig. 1*b*, case A. Here in the upper panel (*a*), the recruits are distributed to regions as (1500, 1000, 500). In case A, shown by the thick, black line with larger solid circles, the *F* values are (0.4, 0.2, 0.1), as in the A cases in Figs. 1*a* and 1*b*. In case B, shown by the grey line with grey solid circles, the *F* values are reversed (0.1, 0.2, 0.4). In the lower panel (*b*), there is directional movement of fish with all the fish recruiting to region 1 and spreading to region 2 and then to region 3 at a rate of 5%·year^{-1}. In case A, shown by the thick, black line with larger solid circles, the *F* values are (0.4, 0.2, 0.1), as in the A cases in Figs. 1*a*, 1*b*, and 2*a*. In case B, shown by the grey line with grey solid circles, the *F* values are reversed (0.1, 0.2, 0.4).



In scenario 4 there was unidirectional dispersion of the fish from region 1 to region 2 to region 3. For case A, in which the rate of fishing mortality was highest in the region that received all the recruits, the population-selection was strongly dome-shaped (Fig. 2*b*, line A); more highly domed than observed in any of the other scenarios we examined. However, in the contrasting case B, in which *F* was lowest in the region receiving the recruits, the population-selection curve took on a form that was neither domed nor asymptotic. It was continuously increasing with peak selection at the oldest age considered in the model. Of all the situations we explored, this was the only case that generated a population-selection curve that was not dome-shaped.

The population-selection curves produced under scenarios 2, 3, and 4 differed in their sensitivity to the value chosen for the movement parameter. When movement was increased to 10%·year^{-1} (not shown in a figure), the curves in scenarios 2 and 3 became markedly less dome-shaped, whereas the domed curve in scenario 4 (case A) became more dome-shaped and the strictly increasing curve (case B) became less curved. To understand these phenomena, consider that nondirectional fish movements, as in scenarios 2 and 3, tend to break down differences in age structure among the spatial subpopulations, with the result that population-selectivity tends to revert to the underlying gear-selectivity. In contrast, directional fish movement, as in scenario 4, accentuates differences in the age structure among the subpopulations, which results in increased divergence between the population-selection and gear-selection curves.

At first glance it seems strange that the population-selection curve, under most circumstances, could be dome-shaped when the underlying gear-selection curves have a strictly asymptotic form. However, the mechanism producing this result becomes clearer if one considers the age-specific fishing mortality curves in the individual regions. For example, the asymptotic F_a curves for two regions with $F = 0.4$ in one region and $F = 0.1$ in the other region are shown (Fig. 3), similar to the configuration in case A of scenario 1. The F_a curve for the population is intermediate between the F_a curves for the two regions. The population-level F_a curve must lie between the regional F_a curves. The higher rate of fishing mortality in the one region results in higher catches of young fish, decreased abundance and catches of older fish in this region, and a reduced contribution to the population-level F_a curve. Thus the population F_a curve is dominated at young ages by the upper F_a curve, but gradually shifts with age to being dominated by the lower F_a curve; it therefore takes on a domed shape. Of course, if there is rapid diffusion of fish among the regions, then the spatial age structuring evaporates and the population-selection curve reverts to the underlying gear-selection curve.

Scenarios 5 and 6 explored the consequences of having more than one gear-selection curve. The simpler scenario (5), which maintained strict regional separation of the two gear types, produced a population-selection curve that had a complex form with three inflection points and an intermediate plateau (Fig. 4*a*). In the other scenario (6), there was mixing of the two gear-selection curves in region 2, so that the composite gear-selection curve for region 2 and the overall population-selection curve both had complex shapes with three inflection points (Fig. 4*b*). In both scenarios the population-selection coefficient for the last age class was less than the population-selection coefficient for the second to last age-class, suggesting that the curves would have been dome-shaped if more age classes had been included.

Discussion

In this study we developed a reasonably simple mathematical representation for population-selectivity, which measures the age-specific rates of fishing mortality experienced by an exploited fish population. The main ingredients of population-selectivity are one or more gear-selection curves, the spatial distribution of the fish, and the spatial distribution of the fishing. When there are multiple types of fishing gear with differing gear-selection curves, then the relative amounts

Fig. 3. Heuristic demonstration of why spatial averaging of asymptotic gear-selection curves results in a population-selection curve that is dome-shaped, indicated by the thick, black line with larger solid circles. Both regions have the same asymptotic gear-selection curve (not shown). The fishing mortality at age in region 1, shown by the thin solid line with open circles, is four times the fishing mortality at age in region 2, shown by the thin grey line with grey solid circles. Region 1, with its elevated rates of fishing mortality at age, contributes more young fish to the overall catch but fewer old fish because the higher F_{age} causes reduced abundance of older fish.

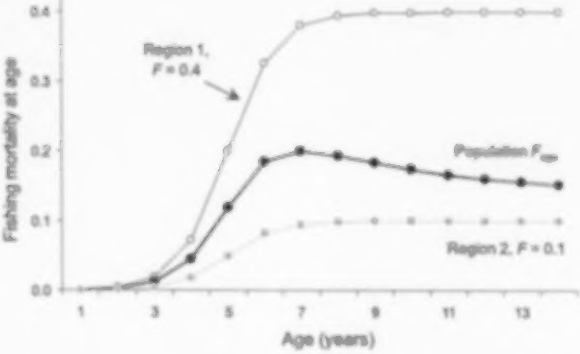
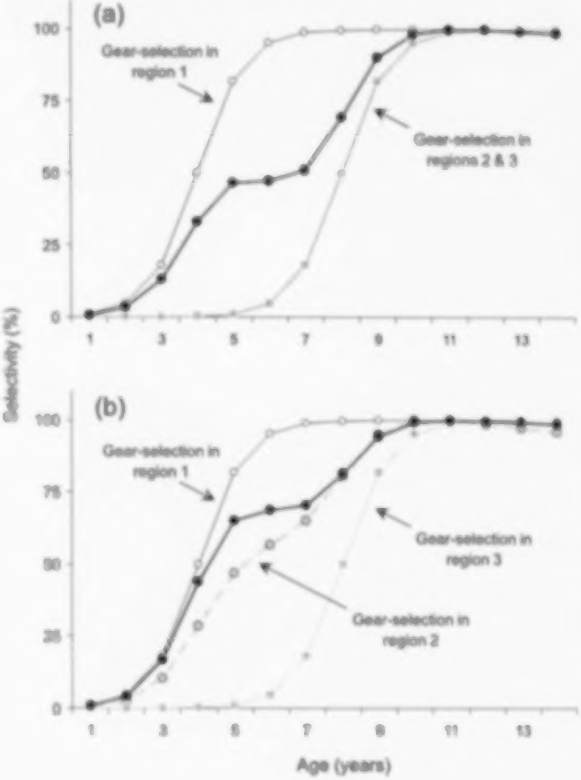


Fig. 4. Population-selection generated from composite gear-selection curves. In the upper panel (*a*) the population-selection curve, shown by the thick, black line with larger solid circles, was generated by a three-region spreadsheet model with two distinct gear-selection curves that were spatially segregated. The configuration was identical to case A in Fig. 1*b*, except that the gear-selection curves for regions 2 and 3 were shifted to the right by four age units. In the lower panel (*b*) the population-selection curve (shown by the thick, black line with larger solid circles) was generated from similar conditions as in panel (*a*), but in region 2 there was 50:50 mixing of the two asymptotic gear-selection curves.



of fishing by the different gear types are an additional influential factor. We demonstrated that this simple model for population-selectivity can generate curves with quite complicated shapes. One emergent property of the model, which we were very surprised to discover, was the capability for completely flat gear-selectivity to generate population-selectivity that decreases with age. We think it extraordinary that the simple mechanism of unevenly distributed fishing mortality will produce domed selectivity over a wide range of circumstances provided the fish population is spatially structured.

Although the population-selectivity model is an equilibrium model that does not directly describe the dynamics of selectivity, one can deduce that the population-selection curve will change with time as the distribution of fishing changes and the fish population consequently undergoes a transition from one steady state to another. As an extreme example, consider what happens in a fishery similar to the one modeled in scenario 4, where there is slow directional movement of the fish between regions. If the regional rates of fishing mortality are all equal, then the population-selection curve will have the same form as the asymptotic gear-selection curve. However, if there was an abrupt change in the distribution of fishing similar to what was modeled in case A, with a higher *F* value in the region that receives all the recruitment, then the population-selection curve would undergo a transition to a domed curve as it evolved towards its new equilibrium form. If there was an additional abrupt change in the regional *F* values so that the region receiving all the recruitment now had the lowest rate of fishing, then the population-selection curve would undergo an additional transition to a strictly increasing form. That population-selection curves are sensitive to the regional distribution of fishing mortality implies that any factors causing fishing effort to redistribute in space (e.g., changes in fish prices or fishing costs; Sampson 1991) will also cause temporal changes in population-selectivity. Given that most fish stocks exhibit spatial structure and given that the spatial distribution of fishing is variable in time, it seems that having a constant population-selection curve is more likely to be an exception rather than the rule.

The population-selectivity model has important implications regarding what stock assessment models assume about selection coefficients. Because these coefficients modulate the instantaneous rate of mortality experienced by a fish stock, they play a central role in the models of stock dynamics that underlie age-structured stock assessments. In developing our model of population-selectivity, we assumed values for the gear-selection coefficients and derived the resulting population-selection coefficients. An age-structured stock assessment turns this around and estimates parameter values (possibly including the selection coefficients) from observed values of catch-at-age (or catch proportions-at-age).

Assessments based on virtual population analysis (VPA) (Gulland 1965) and its modern successors directly provide scaled estimates (F_{age}) of the population-selection coefficients. In general the VPA methods impose few constraints on selectivity. However, it is common practice to configure a VPA so that the estimates of F_{age} each year are the same for the two oldest age classes. While it may be reasonable on theoretical grounds to assume that gear-selectivity is constant for the oldest age classes (e.g., if selection is size-based and there is little change in size with age), our population-selectivity model indicates that over a wide range of conditions, flat gear-selectivity will produce declining population-selectivity unless the fishing mortality has been applied uniformly across spatial regions, which seems an unlikely event. Hence, for a wide range of general conditions, population-selectivity is probably more likely to be domed than asymptotic. It would be instructive to explore the sensitivity of VPA results to underlying assumptions about selectivity.

In contrast with VPA, assessments based on statistical catch-at-age (SCAA) methods are often applied to catch-at-age data that have been partitioned into separate matrices for two or more distinct fleets, with each fleet having its own selection curve determined by a small set of unknown parameters (Quinn and Deriso 1999). When the data are partitioned by fleet, the SCAA methods estimate gear-selection coefficients for each fleet and no estimates of population-selectivity are required. Partitioning the catch-at-age data in this manner avoids the problem of changes in population-selectivity when there are changes in the relative rates of fishing by the different fleets. SCAA models therefore do not need to account for mixtures of gear-selection curves (e.g., scenarios 5 and 6), provided the catch-at-age data have been suitably partitioned. However, SCAA models do need sufficient flexibility to account for the distortions that arise when the spatial application of fishing mortality is uneven or variable through time. A major premise in many SCAA models is that fleet-level selectivity remains constant for extended periods, except possibly for a small number of abrupt changes between periods. The validity of this assumption often remains untested. If an SCAA model assumes that selectivity is time-invariant when in fact it is changing, the resulting suite of assessment estimates can be quite badly biased (Sampson 1993). Applications of SCAA models should explore the sensitivity of their results to assumptions regarding time-invariant selection curves.

The population-selectivity model also has important implications for conducting simulation-based management strategy evaluations (MSEs), which in recent years increasingly have been used as a tool for risk evaluation and decision analysis in fisheries management (Butterworth and Punt 1999; DeOliveira et al. 2008). The MSE process uses simulation testing to investigate the expected performance of a specified management strategy given a range of plausible alternative scenarios that describe the potential dynamics of the real fishery system. The representation of the underlying fishery system is termed the operating model, and the success (or otherwise) of the MSE framework depends on the extent to which the true range of uncertainty can be identified and represented in the suite of operating models investigated. Variability in selectivity is not always explicitly considered in MSEs. Where it has been included, it has often been implemented as a randomly varying quantity based on historic observations. The possibility for temporal shifts in population-selectivity is rarely, if ever, considered. The behavior of our population-selectivity model indicates that variability in gear-specific effort levels and geographic distribution will cause changes in population-selectivity. When developing MSEs, the potential for shifts in the population selectivity should be carefully considered and where appropriate should be adequately accounted for in the operating model.

The issue of whether selectivity is asymptotic or dome-shaped is sometimes controversial in stock assessments and subsequent calculations of catch quotas (e.g., Butterworth and Rademeyer 2008). If the population-selectivity curve is highly domed, then exploitation of the oldest age classes is relatively light, with the consequence that the stock in equilibrium has a residual pool of spawning stock biomass and can therefore support higher rates of fishing. This "cryptic" biomass is unobserved in the fishery because of the low selectivity of older fish (Fonteneau 1996). If an assessment estimates that population-selectivity is domed when in fact selectivity is asymptotic, then the resulting forecasts for future total allowable catches can be much too high. If these target catches are achieved then overfishing could result. Hence there can be considerable concern when an assessment indicates a dome-shaped selection curve, especially if there are no obvious mechanisms to account for the apparent deficit of older fish in the catches. Our model for population-selectivity, however, demonstrates that across a wide range of general conditions, the simple mechanism of non-uniform fishing will tend to cause selectivity to be dome-shaped. Stock assessment scientists who assume by default that selectivity is asymptotic should reconsider the validity of such an approach.

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Appendix A: Conditions producing domed selectivity

Under equilibrium conditions (constant recruitment and constant rate of fishing mortality), the population-selection curve is dome-shaped if $N_a N_{a+2} > (N_{a+1})^2$. We now prove that this condition leads directly to inequality 6 for the special case of no fish movement between the regions ($P_{ij} = 0$ for all i and j) and identical gear-selection coefficients for three adjacent age classes ($s_a = s_{a+1} = s_{a+2} = s$). We start with the simplest case of two regions and then extend the proof to three regions. The approach can be further extended in the same manner to any number of regions.

With two regions (under the conditions given above), the following equations define population abundance for ages a, $a+1$, and $a+2$.

$$N_a = \sum_{r=1}^{2} N_{a,r} = N_{a,1} + N_{a,2}$$

$$N_{a+1} = \sum_{r=1}^{2} N_{a+1,r} = N_{a,1}\exp(-F_1 s - M) + N_{a,2}\exp(-F_2 s - M)$$

$$N_{a+2} = \sum_{r=1}^{2} N_{a+2,r} = N_{a,1}\exp(-2F_1 s - 2M) + N_{a,2}\exp(-2F_2 s - 2M)$$

In each region the fish that are a+2 years old have suffered 2 more years of mortality than the fish that are a years old. The condition for decreasing population-selectivity is $N_a N_{a+2} > (N_{a+1})^2$, equivalent to $N_a N_{a+2} - (N_{a+1})^2 > 0$.

$$N_a N_{a+2} = (N_{a,1})^2 \exp(-2F_1 s - 2M) + (N_{a,2})^2 \exp(-2F_2 s - 2M) + N_{a,1} N_{a,2} \exp(-2F_1 s - 2M) \\ + N_{a,1} N_{a,2} \exp(-2F_2 s - 2M)$$

$$(N_{a+1})^2 = (N_{a,1})^2 \exp(-2F_1 s - 2M) + (N_{a,2})^2 \exp(-2F_2 s - 2M) + 2N_{a,1} N_{a,2} \exp(-F_1 s - F_2 s - 2M)$$

Note that the first two terms in these last two equations are the same and cancel in the difference.

$$N_a N_{a+2} - (N_{a,1})^2 = N_{a,1} N_{a,2} \exp(-2M)[\exp(-F_2 s) - \exp(-F_1 s)]^2$$

With three regions (under the same conditions) the following equations apply:

$$N_a = \sum_{r=1}^{2} N_{a,r} + N_{a,3} = A + N_{a,3}$$

$$N_{a+1} = \sum_{r=1}^{2} N_{a+1,r} + N_{a,3} \exp(-F_3 s - M) = B + N_{a,3} \exp(-F_3 s - M)$$

$$N_{a+2} = \sum_{r=1}^{2} N_{a+2,r} + N_{a,3} \exp(-2F_3 s - 2M) = C + N_{a,3} \exp(-2F_3 s - 2M)$$

The summation term in each equation represents the abundances for the first two regions. In terms of the condition for decreasing population-selectivity, these equations result in the following set of equations:

$$N_a N_{a+2} = AC + AN_{a,3} \exp(-2F_3 s - 2M) + CN_{a,3} + (N_{a,3})^2 \exp(-2F_3 s - 2M)$$

$$(N_{a,1})^2 = B^2 + 2BN_{a,3} \exp(-F_3 s - M) + (N_{a,3})^2 \exp(-2F_3 s - 2M)$$

$$N_a N_{a+2} - (N_{a,3})^2 = AN_{a,3} \exp(-2F_3 s - 2M) - 2B \exp(-F_3 s - M) + CN_{a,3} + AC - B^2$$

$$N_a N_{a+2} - (N_{a,3})^2 = N_{a,1} N_{a,3} \exp(-2M)[\exp(-F_1 s) - \exp(-F_3 s)]^2 + N_{a,2} N_{a,3} \exp(-2M)[\exp(-F_2 s) - \exp(-F_3 s)]^2 \\ + N_{a,1} N_{a,2} \exp(-2M)[\exp(-F_1 s) - \exp(-F_2 s)]^2$$

The same process can be repeated for a system with four regions and so on.

Pink salmon (*Oncorhynchus gorbuscha*) osmoregulatory development plays a key role in sea louse (*Lepeophtheirus salmonis*) tolerance

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Abstract: Sea lice (*Lepeophtheirus salmonis*) of fish-farm origin have been implicated in reducing populations of pink salmon (*Oncorhynchus gorbuscha*) in British Columbia's Broughton Archipelago. Owing to the physically disruptive nature of louse attachment to fish skin in a hyperosmotic environment, we hypothesize that the impacts on fish performance are ionoregulatory in origin. Therefore, ionoregulatory status was measured in juvenile pink salmon artificially infected in the laboratory and naturally infected in the wild. Body $[\text{Na}^+]$ of laboratory-infected fish (~1 week seawater (SW); 0.2–0.4 g) increased significantly by 12% with a single chalimus-4 louse, and by 23% with 2–3 chalimus-3 lice. Mortality over this 24-day trial was 2.4% for fish initially infected with 1–3 lice. Body $[\text{Na}^+]$ for fish caught with natural infections (~4–12 weeks SW; 0.5–1.5 g) did not differ from uninfected controls. Combining data sets revealed a "no effect" threshold of 0.5 g for body $[\text{Na}^+]$ of fish infected with one chalimus-4 louse. We propose that this size-related louse tolerance is associated with hypo-osmoregulatory development, adding to a previously suggested multifactorial mechanism based on epidermal and immune system development. We suggest management bodies consider this fish-mass threshold when planning to minimize risk to wild fish populations.

Résumé : Les poux de mer (*Lepeophtheirus salmonis*) provenant de piscicultures ont été impliqués dans la réduction des populations de saumons roses (*Oncorhynchus gorbuscha*) dans l'archipel de Broughton en Colombie-Britannique. À cause de la nature perturbatrice de type physique de la fixation des poux à la peau des poissons en milieu hyperosmotique, nous posons l'hypothèse selon laquelle les impacts sur la performance des poissons se font au niveau de la régulation ionique. Le statut d'ionorégulation a été mesuré chez de jeunes saumons roses infectés artificiellement au laboratoire et d'autres infectés naturellement dans le milieu. Le $[\text{Na}^+]$ corporel des poissons infectés en laboratoire (~1 semaine en eau de mer (SW); 0,2–0,4 g) augmente significativement de 12 % en présence d'un seul pou de stade chalimus 4 et de 23 % avec 2–3 poux de stade chalimus 3. La mortalité durant ce test de 24 jours est de 2,4 % chez les poissons infectés initialement avec 1–3 poux. Le $[\text{Na}^+]$ corporel des poissons capturés porteurs d'infections naturelles (~4–12 semaines en SW; 0,5–1,5 g) ne diffère pas de celui des témoins non infectés. Une combinaisons des ensembles de données indique l'existence d'un seuil « d'absence d'effet » de 0,5 g en ce qui a trait au $[\text{Na}^+]$ corporel chez des poissons infectés avec un pou de stade chalimus 4. Nous croyons que cette tolérance aux poux reliée à la taille est associée au développement de l'hypo-osmorégulation, ce qui s'ajoute au mécanisme multifactoriel suggéré antérieurement basé sur le développement de l'épiderme et du système immunitaire. Nous suggérons aux agences de gestion de tenir compte de ce seuil de masse des poissons lorsqu'ils cherchent à minimiser le risque aux populations naturelles.

[Traduit par la Rédaction]

Introduction

The ectoparasitic salmon louse *Lepeophtheirus salmonis* has been recently implicated in pink salmon (*Oncorhynchus gorbuscha*) population declines and extinction predictions in British Columbia's Broughton Archipelago (Morton and Routledge 2005; Krkosek et al. 2007, 2009). Although these studies are compelling, major questions regarding parasite transmission and infection impacts on host physiology remain unresolved. The uncertainty has led to considerable debate as to whether sea lice, specifically of farm origin, are negatively impacting local pink salmon populations (Brooks and Stucchi 2006; Brooks and Jones 2008; Krkosek et al. 2008). A critical knowledge gap that this study aims to address is the level of louse infection required to sublethally impair the performance of the smallest out-migrating juvenile pink salmon, i.e., those weighing between 0.2 g and 2.0 g.

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Lice feed on host mucus, epidermal tissue, and blood (Kabata 1974; Brandal et al. 1976) as they grow in size and develop through four attached stages (termed chalimus 1–4) and three motile stages (termed pre-adult 1–2 and adult) on the fish's exterior surface (Johnson and Albright 1991; Tully 1992; Brooks 2005). As shown in 200 g Atlantic salmon and 90 g sea trout, this surface feeding can lead to significant increases in plasma electrolytes (up to 60%; Grimnes and Jakobsen 1996; Bjorn and Finstad 1997; Nolan et al. 1999). This hydromineral disruption is thought to result either directly from epidermal lesions that damage the external osmotic barrier, or indirectly from a stress-related increase in the osmorespiratory compromise (Gonzalez and McDonald 1992; Gonzalez and McDonald 1994; Wendelaar Bonga 1997). Regardless of origin, hydromineral imbalance is considered a major concern, as it can stunt growth (Brauer 1982; Folmar et al. 1982; McCormick et al. 1987), reduce swim performance (Brauner et al. 1992, 1994), and even cause death (Boeuf and Harache 1982).

Adult pink salmon are likely well equipped to cope with parasitism in the wild (~50 lice per fish; Beamish et al. 2005), but out-migrating juveniles are likely less prepared for a number of reasons. Foremost of these is that pink fry enter seawater as small as 0.2 g (Heard 1991), and are thus three orders of magnitude smaller than adult fish when first exposed to sea lice (Jones and Hargreaves 2007). Thus, their surface area to volume ratio is much higher, which is a major factor for ion and water exchange with the environment. Additionally, the epidermal (Jones et al. 2008*a*), immune (Johnson et al. 1982) and hypo-osmoregulatory (Grant et al. 2009) systems of pink salmon are all still developing during the first few months in seawater. Since these physiological characteristics are presumably critical to their resistance to and tolerance of infection with *L. salmonis*, juvenile pink salmon are likely particularly vulnerable to ectoparasites such as sea lice during their initially precocious out-migration.

Currently, only one study has quantified the sublethal effects of infection on out-migrating (0.2–3.0 g) pink salmon. One motile louse was shown to significantly reduce the swimming performance of fish with a body mass of less than 0.7 g (Nendick et al. 2011). Interestingly, this body-mass threshold for the impairment of swimming performance corresponds with the body mass when pink salmon complete hypo-osmoregulatory development (0.7–1.0 g; Grant et al. 2009), suggesting that the observed effects on swimming are perhaps linked to impaired hypo-osmoregulatory ability. Indeed, swimming performance was similarly reduced with elevated plasma ions in larger *O. kisutch* (8–20 g) following seawater entry (Randall and Brauner 1991; Brauner et al. 1992, 1994) and with larger *Salmo salar* (600 g) infected with 80 lice per fish (Wagner et al. 2003, 2004). Furthermore, louse-infected *S. salar* (200 g) have been shown to upregulate gill Na^+/K^+-ATPase (NKA) activity by as much as 60% (Nolan et al. 1999), likely as an attempt to restore hydromineral balance. Based on these findings, we hypothesize that louse-induced performance reductions may be ionoregulatory in origin.

Thus, the objective of this study was to quantify the ionic disruptions and ionoregulatory compensations associated with ecologically relevant louse infection levels (1–3 *L. salmonis* per fish) in post-emergent juvenile pink salmon (0.2–1.5 g). Ionoregulatory status was measured in three separate series of fish: (*i*) laboratory-infected, naïve fish collected from the Glendale River (~0.2–0.4 g), (*ii*) naturally infected, ocean-caught fish collected from the Broughton Archipelago (~0.5–1.5 g), and (*iii*) uninfected, naïve fish subjected to various degrees of experimenter-induced epidermal abrasion (~0.7 g). Data for infected fish from the first two series were combined to determine a threshold fish mass for sublethal louse effects. This threshold could prove to be useful for fisheries managers when planning to minimize risk to wild populations.

Materials and methods

Research facility

All experiments were conducted at an autonomous field laboratory in the Broughton Archipelago, British Columbia, Canada, between March and July of 2008. Constructed on a float-house adjacent to Doctor Islets in Knight's Inlet, the laboratory location provided easy access to wild juvenile pink salmon throughout the entirety of their near-shore migration (transport time from collection areas never exceeded 4 h). Laboratory holding tanks were equipped with flow-through aerated seawater (SW) drawn from depth at 30 m to ensure stable temperature (7.0–8.5 °C) and salinity (32–34 ‰), and the facility's translucent canopy permitted a natural photoperiod throughout study duration. All fish were treated in accordance with the University of British Columbia Animal Care Committee and the Canadian Council on Animal Care.

Series 1: Controlled laboratory infection of river-caught fish

Experimental animals

River-caught fish

Approximately 2000 post-emergent pink fry were collected with rotary screw-traps from the Glendale River during their down-stream migration on 27 March 2008. Fish were immediately transported to the field laboratory where they were gradually exposed to full strength SW (34 ‰) over a period of 24 h. Initially at an approximate size of 25 mm and 0.2 g, pink fry were divided into four 100 L fibreglass holding tanks in which they were fed, and readily accepted, commercial trout chow twice daily (Bio-Vita starter feed; Bio-Oregon, Longview, Washington, USA). Glendale River was selected as a fish source because it is highly representative of the region's pink salmon productivity, accounting for more than 35% and 85% of total Broughton pink salmon in even and odd years, respectively (Brooks and Jones 2008). Out-migrating river caught (RC) fish were used for laboratory-based infections for two reasons: (*i*) they had no prior exposure to sea lice; and (*ii*) they represented the earliest and presumably most sensitive life-stage that could become infected in the wild given their precocious seawater entry.

Lepeophtheirus salmonis

Approximately 300 gravid female lice were collected from adult Atlantic salmon on 24 March 2008 during a commercial harvest at Marine Harvest Canada's Wicklow Point farm. Upon transport to the Doctor Islets laboratory, louse egg strings were incubated at 7 °C in four 4 L closed containers filled with aerated SW (34 ‰). Active nauplii were filtered out every 2 days with 96 µm plankton mesh and placed in separate 2 L rearing chambers. Incubation water was changed every other day and nauplii monitored daily for copepodid development. Active copepodid densities were estimated by averaging counts from five 10 mL aliquots sampled from each rearing chamber. Infection was initiated when a copepodid:nauplii ratio of 3:1 was reached.

Infection protocol and results

Infection of pink salmon with *L. salmonis* was initiated on 3 April 2008 after RC fish had spent 1 week in SW. A total of 581 fish was divided into subgroups of ~75 and placed into 8 separate 11 L infection chambers (modified POS plastic totes; Rubbermaid). Each chamber was filled with 3 L of static aerated SW and approximately 1700 active copepodids, yielding a bath density of ~560 copepodids·L^{-1} and a copepodid:fish ratio of 23:1. Chamber dimensions were such that the infection bath depth was only 5 cm, minimizing fish–louse stratification and maximizing host–parasite interaction. Louse exposure was carried out in darkness for a total of 4 h, followed by a switch to flow-through SW to flush the infection bath. An additional 150 fish were subjected to an identical sham infection without lice and used as the control.

Approximately 48 h post-infection, all fish were lightly anaesthetized (0.05 g tricaine methanesulfonate (MS-222)·(L saltwater)$^{-1}$) and sorted according to louse load. Out of 581 fish, 511 were successfully infected with at least one louse (a prevalence of ~88%). Of these, 129 individuals (22%) were infected with 1 louse, 101 individuals (17%) with 2 lice, 99 individuals (17%) with 3 lice, and 182 individuals (31%) were infected with 4+ lice (up to 20 lice were present on some fish). Fish that remained uninfected following louse-exposure were not used. Following sorting, fish were placed in 10 separate 11 L holding tanks according to five categories of louse load (0, 1, 2, 3, and 4+ lice per fish; 2 replicate tanks per treatment). Each tank was equipped with flow-through SW (34 ‰, 7.0–8.5 °C), held no more than 75 fish and was supplied with commercial trout chow twice daily. The tanks with 4+ lice per fish were used only as a backup supply (see below).

Sampling protocol and constraints

Fish were sampled over the ensuing 24 days as sea lice matured towards adult stages. For the experiments described below, a total of 20 fish (10 for whole body [Na^+] and 10 for gill NKA activity) were sampled for each of four louse loads (0, 1, 2, and 3 lice per fish) at each of four development stages for an attached louse [chalimus stages 1 through 4, which represented 3, 7, 15, and 24 days post-infection (DPI), respectively]. All fish were examined by microscope at the time of sampling to determine the exact louse number, developmental stage and surface area of exposed subepidermal tissue. Subepidermal tissue exposure was quantified by overlaying a microscope slide equipped with a 1 mm × 1 mm grid on the louse wound. Subepidermal tissue in this case is defined as the flesh immediately beneath the scales and thin outer dermis.

As reported in recent laboratory studies (Jones et al. 2008*a*, 2008*b*), infected pink salmon fry experienced high rates of louse loss throughout trial duration. Consequently, the number of infected fish (especially those with more than one louse) declined over time. As a result, actual louse loads on fish did not always match the designated tank load from the initial fish sorting completed 48 h post-infection. On sampling days, fish were drawn randomly from all treatment tanks to find appropriate louse loads, which obviated a repeated sampling design. Furthermore, to compensate for louse loss, the back-up supply of the 4+ lice per fish group were resorted at 14 DPI (~chalimus-3 stage) and redistributed among the 1–3 lice per fish treatment tanks. A total of 99 fish were added to the sampling population (48 fish with 1 louse, 31 fish with 2 lice, and 20 fish with 3 lice). Even with these additions, infected fish numbers remained limited; hence, measurements of gill NKA activity were necessarily restricted to fish with 1–2 lice of chalimus stages 1–3, while measurements of whole body [Na^+] beyond the chalimus-3 stage were limited to fish with 1 louse.

As mentioned above, all reported louse loads correspond to infection levels at the time of sampling and not the initial sort completed 48 h post-infection. Owing to the high levels of louse loss, louse loads for some individuals would have been higher prior to sampling. Thus, the impacts of specific louse loads reported here would tend to overestimate rather than underestimate an impact for a given reported louse load.

Series 2: Natural infection of ocean-caught fish

Over 10 000 wild pink salmon fry were captured by beach or purse seine during their near-shore migration through the Broughton Archipelago between April and June of 2008. These ocean-caught (OC) fish were graded directly following collection, so that excess, uninfected fish could be released immediately, whereas louse-infected fish could be transported promptly to the field laboratory. Fish were permitted a 24-h recovery period in the laboratory, then lightly anaesthetized (0.05 mg MS-222·(L seawater)$^{-1}$; Syndel) for sorting according to louse number and developmental stage. After an additional 24-h recovery period, fish were sampled for assessments of whole body [Na^+] and (or) gill NKA activity, and the area of subepidermal tissue exposure was measured in both control and infected fish as in Series 1. To minimize the potential for confounding effects, fish were sampled to provide at least eight infected, similarly sized fish with a similar louse developmental stage that were collected at the same location on the same date. This sampling regime was designed to minimize any variation attributable to fish development and environmental experience. These criteria, combined with a low infection intensity among OC fish (total louse prevalence was roughly 10%, with an intensity of approximately 1), restricted analysis to fish infected with 1 attached chalimus stage louse. As with Series 1, assay priority was given to whole body [Na^+] analysis. Three size ranges of infected OC fish were obtained in sufficient number for analysis (~0.5 g, 1.0 g, and 1.5 g). A group of 10 uninfected, size-matched fish were used as a control for each range.

Series 3: Experimenter-induced epidermal abrasion of river-caught fish

In response to the low mortality and high louse loss observed in the laboratory infections of Series 1, low levels of infection and epidermal damage observed in the natural infections of Series 2 and a general lack of advanced infections in both series, uninfected RC fish were subjected to a "worst case" scenario in an attempt to elicit negative effects thought to be associated with more severe louse infection. Because this series was conceived in response to observations in Series 1 and 2, our RC laboratory pink salmon population had already grown considerably. Therefore, the smallest fish size available was approximately 0.7 g.

To mimic mechanical skin damage inflicted by motile sea lice, the epidermis of uninfected RC fish acclimated to SW were subjected to various degrees of artificial abrasion following completion of Series 1. Using even pressure with a No. 2 scalpel blade, lightly anaesthetized fish (approximately 0.7 g and 50 mm in size) were subjected to the following: (*i*) 1 mm^2 scale removal, (*ii*) 1 mm^2 subepidermal tissue exposure, or (*iii*) 2 mm^2 subepidermal tissue exposure. The surface areas for abrasion were selected to match motile louse mouth sizes, and fish size corresponded to when wild fish might first encounter a motile sea louse in 2008. All lesions were located posterior to the dorsal fin on the lateral line, and abrasion time never exceeded 30 s. A sham group was abraded in an identical fashion with the scalpel handle to serve as a control. 1 mm^2 scale removal is defined as the removal of scales from an area of 1 mm^2; subepidermal tissue exposure is defined above (see Series 1).

Following abrasion, fish were held in duplicate tanks for each of the four treatment groups. Holding tanks, water conditions, and fish care were identical to those of Series 1. For whole body [Na^+] and gill NKA activity, a total of 20 fish from each treatment were sampled pre-abrasion, and at 1 and 5 days post-abrasion as described below. Gill NKA activity was not measured in the 2 mm^2 abrasion group, owing to the limited availability of fish.

Assays

Wet and dry mass, and total body [Na^+]

Fish were anaesthetized with a lethal dose of buffered MS-222 (0.8 $g \cdot (L\ seawater)^{-1}$; Syndel Laboratories, Vancouver, British Columbia, Canada), rinsed in de-ionized water, blotted dry, and weighed for wet body mass. Individual fish were subsequently dried at 65 °C to a constant dry mass and digested in 1 $mol \cdot L^{-1}$ nitric acid (1 mL of acid for every 0.1 g of wet tissue mass). Digest supernatant was subsequently analyzed for Na^+ concentration ([Na^+]) using flame atomic absorption spectroscopy (Spectra AA-220FS; Varian, Mulgrave, Victoria, Australia). Total body [Na^+] is reported as $\mu mol\ Na^+ \cdot (g\ wet\ mass)^{-1}$.

Gill Na^+/K^+-ATPase activity (NKA)

Whole gills were removed from lethally anaesthetized fish (see above) and stored at –80 °C. A modified version of the method outlined by McCormick (1993) was used to determine gill NKA activity. Briefly, individual whole frozen gills were homogenized on ice in SEI buffer (250 $mmol \cdot L^{-1}$ sucrose, 10 $mmol \cdot L^{-1}$ EDTA, 50 $mmol \cdot L^{-1}$ imidazole; pH 7.3). Homogenates were centrifuged at 5000*g* for 1 min and the supernatant placed on ice. Supernatant ATPase activity was measured spectrophotometrically in the presence and absence of ouabain (1 $mmol \cdot L^{-1}$), and taken as the difference between conditions. Protein concentration was measured using the bicinchoninic acid method (Sigma-Aldrich) with bovine serum albumin standards. NKA activity is reported as $\mu mol\ ADP \cdot (mg\ protein)^{-1} \cdot h^{-1}$.

Statistical analyses

Data are expressed as mean values ± standard error of the mean (SEM). A two-way analysis of variance (ANOVA) was used throughout to determine significant differences, and the Holm–Sidak post-hoc test was subsequently applied for pairwise comparisons. Second order polynomial regression lines were fitted to pooled data sets for infected and uninfected fish to estimate a threshold fish mass for louse effects. All data passed tests for normality and homogeneity of variance. All statistical analyses were conducted with Sigmastat (version 3.0, Systat Software Inc., San Jose, California, USA), and a significance level of $P < 0.05$ was used throughout.

Results

Series 1: Controlled laboratory infection of river-caught fish

Fish mortality, fish growth and epidermal damage by lice

Mortality among fish originally infected with 1–3 lice per fish was 2.4% (8 of 329 fish). Ninety-nine fish originally infected with 4 or more lice were added to the 1–3 lice per fish group at 14 DPI following a re-sort of infected fish (see methods). From the combined 428 fish, 25 died during the 24-day trial. Since there was no mortality among control fish, overall louse-induced mortality was 5.8%. However, of these 25 dead fish, 17 originated from the 4+ lice per fish group, which could have had an initial infection of as many as 20 lice per fish.

Control fish grew significantly from 0.224 ± 0.014 g to 0.358 ± 0.019 g over a 24-day period ($P < 0.001$, $t = 6.376$), yielding a specific growth rate (SGR) of 2.26 ± 0.66% $body\ mass \cdot day^{-1}$ (Table 1). Infected fish grew at a similar rate, with SGR ranging from 1.23% $body\ mass \cdot day^{-1}$ to 1.86% $body\ mass \cdot day^{-1}$. Fish mass differed significantly from the control group at 7 DPI in the 2 lice per fish treatment ($P = 0.027$, $t = 2.241$; Table 1), but had recovered by 15 DPI.

Superficial, louse-inflicted epidermal damage was visible on host fish as early as 3 DPI (chalimus-1 stage) and subepidermal tissue was exposed by 15 DPI (chalimus-3 stage; Table 1) with just one louse per fish. The area of exposed subepidermal tissue significantly increased (3-fold) between 15 and 24 DPI in the 1 louse per fish treatment ($P = 0.18$, $t = 2.403$; Table 1), during which time lice developed from the chalimus-3 to chalimus-4 stage. No significant differences among louse loads were resolved ($P > 0.05$).

Total body [Na^+] and gill Na^+/K^+-ATPase

ANOVA revealed that both DPI and louse load had significant effects on total body [Na^+] ($P = 0.007$, $F = 3.671$ for DPI; $P < 0.001$, $F = 5.804$ for load) and on gill NKA activity ($P < 0.001$, $F = 27.745$ for DPI; $P < 0.001$, $F = 11.49$ for load) of RC fish. A statistically significant interaction between DPI and louse load was also found for both total body [Na^+] and gill NKA activity ($P < 0.001$ for each).

As expected of a normal pink salmon developmental trajectory in SW (see Grant et al. 2009), total body [Na^+] of control fish decreased steadily and significantly from

Table 1. Fish mass and quantified area of exposed sub-epidermal tissue in controlled laboratory infection of river-caught fish (Series 1).

DPI, stage	Specified damage	Control	1 Louse	2 Lice	3 Lice
Day 0	Mass (g)	0.224±0.014	NA	NA	NA
	Tissue damage (mm^2)	0			
Day 3, C1	Mass (g)	0.243±0.009	0.224±0.011	0.234±0.009	0.235±0.008
	Tissue damage (mm^2)	0	0	0	0
Day 7, C2	Mass (g)	0.272±0.011	0.254±0.016	0.231±0.015*	0.249±0.010
	Tissue damage (mm^2)	0	0	0	0
Day 14, C3	Mass (g)	0.283±0.010	0.313±0.015	0.279±0.019	0.259±0.014
	Tissue damage (mm^2)	0	0.10±0.05a	0.20±0.06ab	0.15±0.06ab
Day 24, C4	Mass (g)	0.358±0.019	0.336±0.031	NA	NA
	Tissue damage (mm^2)	0	0.30±0.08b		
Specific growth rate (%)		2.26±0.66 over 24 days	1.86±1.00 over 24 days	1.48±0.86 over 14 days	1.23±0.34 over 14 days

Note: Values are the mean ± SEM; sample size = 10; DPI, days post infection; C1–C4, chalimus developmental stages 1–4; NA, not available; * indicates significant differences from time-matched controls for fish mass; different letters indicate statistically significant differences from time-matched controls for tissue damage ($P \leq 0.05$). Specific growth rate is calculated as percent body weight per day.

81 μmol·g^{-1} at 0 DPI (1 week following SW transfer) to 73 μmol·g^{-1} by 24 DPI ($P = 0.006$, $t = 2.770$; Fig. 1*a*). Total body [Na$^+$] of fish infected with one louse did not differ significantly from control values until 24 DPI [chalimus-4 stage, Fig. 1*a*; $P = 0.01$, $t = 2.611$], when a 12% increase was observed. A larger and earlier increase in total body [Na$^+$] occurred in fish infected with two and three lice, where a 23% increase was observed by 15 DPI [chalimus-3 stage, Fig. 1*a*; $P < 0.001$, $t = 4.99$ for two lice; $P < 0.001$, $t = 4.348$ for three lice]. Thus, all three infection loads had a threshold louse developmental stage beyond which a significant ionic disturbance was triggered. This developmental threshold was advanced when fish hosted more than one louse (two lice triggered a greater ionic disturbance than one louse) but the effect was not necessarily additive (total body [Na$^+$] did not differ significantly between two and three lice per fish).

As expected of a normal developmental trajectory in SW, gill NKA activity of control fish increased steadily and significantly from 7 μmol ADP·mg^{-1}·h^{-1} at 0 DPI to 11 μmol ADP·mg^{-1}·h^{-1} by 15 DPI [Fig. 1*b*; $P < 0.001$, $t = 3.461$]. For infected fish, however, gill NKA activity was significantly depressed as early as 3 DPI with just one louse [chalimus-1 stage, Fig. 1*b*; $P < 0.001$, $t = 3.565$]. This approximately 40% depression in enzyme activity was maintained independent of louse load through 7 DPI (chalimus-2 stage). By 15 DPI (chalimus-3 stage), gill NKA activity had recovered to control levels in all treatments. Therefore, rather than showing a compensatory increase in association with elevated ionic loads, infected fish exhibited an initial reduction in gill NKA activity.

Series 2: Natural infection of ocean-caught fish

As with laboratory-infected fish (Series 1), subepidermal tissue was not exposed in infected OC fish prior to the chalimus-3 stage. Furthermore, subepidermal tissue was only exposed in the smallest size class of OC fish (0.474 ± 0.043 g).

A two-way ANOVA revealed that body mass had a significant effect on total body [Na$^+$] ($P < 0.001$, $F = 42.782$) and gill NKA activity ($P < 0.001$, $F = 10.216$) of OC fish. Louse load was shown to have no effect ($P = 0.627$, $F = 0.239$ for body [Na$^+$]; $P = 0.332$, $F = 0.957$ for gill NKA activity), and there was no significant interaction between body mass and louse load ($P = 0.332$).

The changes in total body [Na$^+$] and gill NKA activity with body mass of uninfected OC fish followed the same patterns as observed for control fish of Series 1. Over the fish mass ranging from ~0.5 g to ~1.5 g, total body [Na$^+$] decreased significantly from ~70 to ~50 μmol·g^{-1} [Fig. 2*a*; $P < 0.001$, $t = 5.997$]. Correspondingly, gill NKA activity increased significantly from ~10 to ~14 μmol ADP·mg^{-1}·h^{-1} [Fig. 2*b*; $P = 0.016$, $t = 2.480$]. Total body [Na$^+$] and gill NKA activity of infected OC fish did not differ significantly from size-matched, uninfected OC fish (Fig. 2; $P > 0.05$).

Series 3: Experimenter-induced epidermal abrasion of river-caught fish

The area of epidermal abrasion applied to RC fish exceeded the maximum area of louse-induced abrasion by nearly 10-fold (Series 1 and 2). Despite this excessive damage, neither total body [Na$^+$] nor gill NKA activity differed significantly from respective time-matched controls (Fig. 3; $P > 0.05$). Furthermore, total body [Na$^+$] and gill NKA activity were similar to size-matched, control fish in other experiments.

Estimated threshold for louse effect

The data sets for total body [Na$^+$] from laboratory (Series 1) and natural infections (Series 2) overlapped in terms of body mass and could be pooled to determine a body mass threshold for louse-induced ionoregulatory disturbance. Second order polynomial regression lines were fitted to the pooled data sets for uninfected$y = 84.6 - (41.7x) + (12.5x^2)$; $r^2 = 0.87$; $P < 0.001$; $F = 140$) and infected $y = 109.3 - (99.0x) + (43.8x^2)$; $r^2 = 0.89$; $P < 0.001$; $F = 84.5$) fish. Total body [Na$^+$] of fish infected with one chalimus-4 louse was significantly higher than that of uninfected fish below a body mass of 0.5 g (Fig. 4*a*), as clearly indicated by non-overlapping 95% confidence intervals. The observed difference in body [Na$^+$] between infected and uninfected fish below this threshold body mass of 0.5 g de-

Fig. 1. Total body [Na^+] relative to (*a*) fish wet mass and (*b*) gill Na^+/K^+-ATPase activity (*b*) of river-caught fish artificially infected with *L. salmonis* copepodids (triangles, control; white circles, one louse; grey circles, two lice; black circles = three lice). Fish were infected 1 week following transfer to seawater, and sampled over 24 days at times corresponding to each of the four chalimus developmental stages (C1–C4). The vertical broken lines represent approximate moulting events of lice as they develop from the copepodid through each of the chalimus stages (C1–C4). Data points represent mean ± SEM, $n = 10$. Asterisks indicate statistically significant differences from time-matched controls; different letters indicate statistically significant differences within the control group ($P \leq 0.05$).

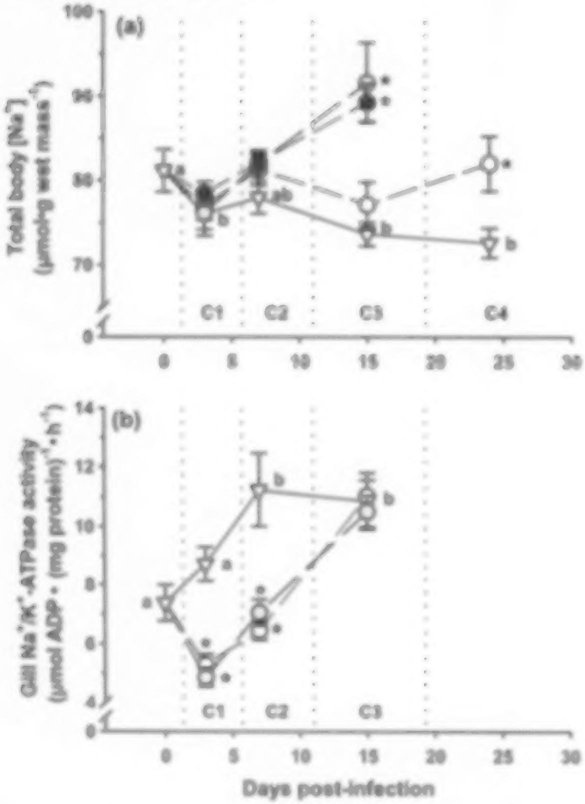
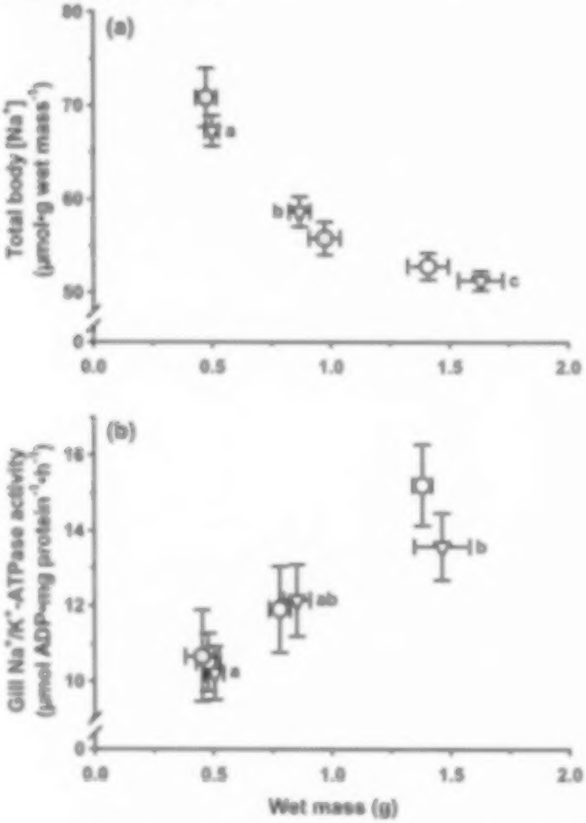


Fig. 2. Total body [Na^+] relative to (*a*) fish wet mass and (*b*) gill Na^+/K^+-ATPase activity of ocean-caught fish naturally infected with one *L. salmonis* chalimus (triangles, control; white circles, chalimus stages 1 and 2; grey circles, chalimus stages 3 and 4). Data points represent mean ± SEM, $n = 10$. Values for infected fish do not differ significantly from size-matched controls; different letters indicate statistically significant differences within the control group ($P \leq 0.05$).



creased with increasing fish mass and gill NKA activity (Figs. 4*a* and 4*b*).

Discussion

Using ecologically relevant infection levels of 1–3 attached-stage lice per fish, we document some of the first sublethal physiological impacts of sea lice on post-emergent pink salmon. We conclude that beyond a threshold fish size of 0.5 g, one attached-stage louse (chalimus stages 1–4) no longer significantly disrupts hydromineral balance. Furthermore, we propose that this body mass threshold is linked to hypo-osmoregulatory development in juvenile pink salmon, which likely plays a key role in coping with the effects of epidermal damage and (or) stress incurred by sea louse infections.

Results from the laboratory infection study clearly show that one louse at the chalimus-4 stage and two to three lice at the chalimus-3 stage are sufficient to significantly disturb total body Na^+ balance in pink salmon weighing less than 0.5 g. Because louse loads decreased over time in many fish, reported infection loads actually underestimated the infection history. Similarly, louse numbers for wild-infected OC fish also could have been greater prior to examination. Consequently, our measures of impact and the identified threshold, if anything, tend to overestimate rather than underestimate an impact for a given reported lice load.

We propose that this size-related louse tolerance is linked to pink salmon hypo-osmoregulatory development, adding to a previously suggested multifactorial mechanism based on epidermal and immune system development (Jones et al. 2008*a*). A primary proximal effect of louse infection is physical damage to the host epidermis (Kabata 1974; Brandal et al. 1976), which can potentially lead to hydromineral imbalance by disrupting the osmotic barrier and (or) inducing a stress response (Wendelaar Bonga 1997). While the immune

Fig. 3. Total body [Na$^+$] relative to (*a*) fish wet mass and (*b*) gill Na$^+$/K$^+$-ATPase activity of river-caught fish following various degrees of mechanical epidermal abrasion (triangles, control; white circles, 1 mm^2 de-scaling; grey circles, 1 mm^2 lesion; black circles, 2 mm^2 lesion). Fish were transferred to seawater 4.5 weeks prior to abrasion. Mean fish mass is 0.738 g ± 0.019 SEM. Data points represent mean ± SEM, n = 10; treatment groups did not differ significantly from control ($P \geq 0.05$).

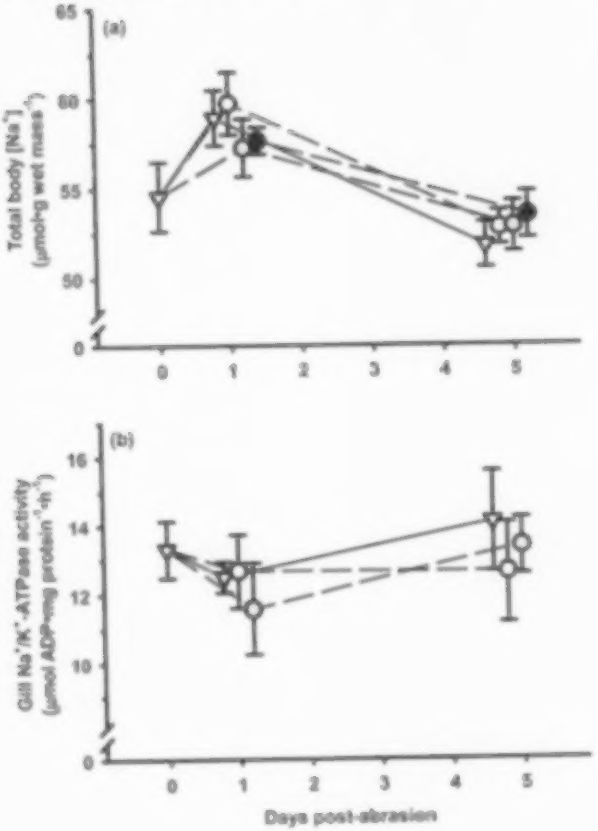
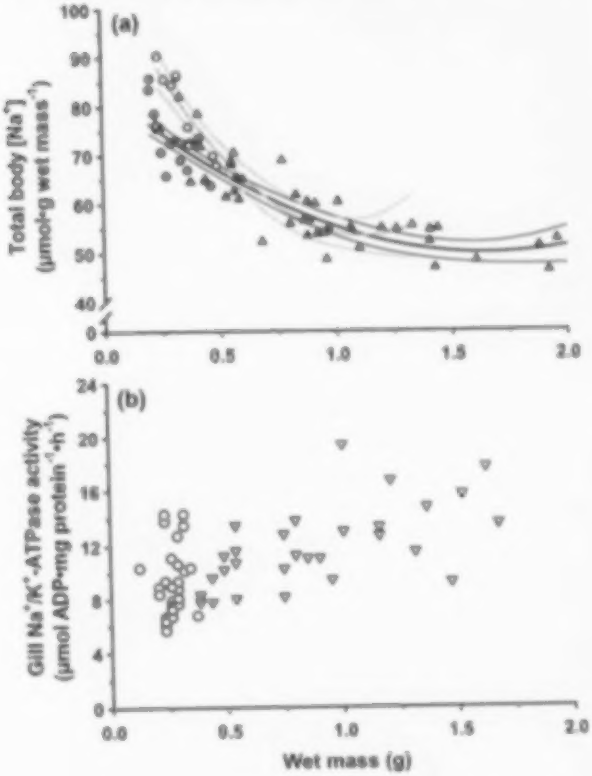


Fig. 4. Total body [Na$^+$] relative to (*a*) fish wet mass and (*b*) gill Na$^+$/K$^+$-ATPase activity of infected (shaded symbols) and uninfected (open symbols) fish. Circles represent individual river-caught fish from Series 1 infected in a laboratory setting, and triangles represent individual ocean-caught fish from Series 2 infected in the wild. All infected fish possess a load of one chalimus-4 louse. Regression lines are second order polynomials based on total uninfected (grey line; $y = 84.6 - (41.7x) + (12.5x^2)$; $r^2 = 0.87$; $P < 0.001$; $F = 140$) and infected (black line; $y = 109.3 - (99.0x) + (43.8x^2)$; $r^2 = 0.89$; $P < 0.001$; $F = 84.5$) fish. Fine lines represent 95% confidence intervals.



system and epidermis combat proximal effects of parasitism (Jones 2001; Jones et al. 2008*a*, 2008*b*), hypo-osmoregulatory ability enables fish to cope with the hydromineral consequences of any epidermal damage or attachment stress that might occur. The inverse relationship between total body Na$^+$ load and gill NKA activity of infected fish supports this notion, as does the absence of any ionic loading beyond attainment of maximum gill NKA activity. Hypo-osmoregulatory advanced fish even maintain Na$^+$ balance despite levels of skin abrasion 10-fold greater than those inflicted by lice. Although the nature of these two types of epidermal damage differs considerably, this result suggests larger-sized pink salmon may better tolerate at least the physical damage associated with louse loads beyond those explored here. Because epidermal damage for a given louse load decreases with increasing fish mass, this finding is also consistent with the proposed role of epidermal and immune system development in louse resistance (Jones et al. 2008*a*).

Louse-induced mortality over 24 days of small, laboratory-infected fish was 2.4% with an initial infection of 1–3 lice per fish, and 5.8% overall when fish previously infected with as many as 4–20 lice were re-sorted at 14 DPI into the 1–3 lice per fish group. Although low, this number could be much higher in the wild if sublethal ionic disturbances observed in the laboratory prove to affect survival in a natural setting. An associated study found reductions in pink salmon swimming performance to occur at infection thresholds similar to those identified here for hydromineral balance (Nendick et al. 2011), indicating that the ion load may indeed impart a performance cost. Negative impacts on fish growth, while not resolved here, may also occur in the wild where active foraging is required for feeding. To better understand the impacts on fish survival in the wild, studies such as those conducted here should be further paired with other surrogate measures of fitness. Lethality could also increase with louse development beyond that studied here, but so would louse loss without re-infection. Clearly, fish growth, louse loss, and louse development are all important interactive factors in assessing the impacts of sea lice on juvenile pink salmon.

The mechanisms through which small juvenile pink salmon cope with a louse-induced ion load remain unclear. As in hydromінerally challenged rainbow trout, other areas of the body could buffer plasma and critical tissue osmolarity (e.g., Wood and Randall 1973*a*, 1973*b*; Bath and Eddy 1979) with associated costs to aerobic scope, energy stores, and (or) recipient buffer tissue function. Any of these impacts could explain the previously reported reductions in swimming ability (Nendick et al. 2011). Even the larger, more developed fish that maintained ion balance following infection and abrasion could be incurring substantial energetic costs. A simple and effective way to quantify the energetic costs associated with louse infection and any resulting ionoregulatory challenge would be to measure resting metabolic rate and metabolic scope in future studies.

Enhanced gill NKA activity of infected fish was predicted as a compensatory response to louse-induced hydromineral disturbance. However, neither louse-infected nor abraded fish showed this response. In fact, gill NKA activity was temporarily lower in laboratory-infected RC fish. Stress-related elevations in cortisol have been previously correlated with similar reductions in gill NKA activity of confined but uninfected chinook salmon (Strange et al. 1978), and louse-infected fish are known to exhibit stressful behaviours to rid themselves of lice (Webster et al. 2007). Therefore, the observed reduction in gill NKA activity could simply be the product of a generalized stress response (Wendelaar Bonga 1997). A stress response might also help explain the lack of ionic load in the epidermal abrasion experiments and the less than additive effects of more than one sea louse on ion balance in the laboratory infections. Nevertheless, an equally plausible explanation is that sea lice preferentially infect weaker and less developed fish. An unavoidable limitation to studying louse impacts is the inability to control which fish become infected and retain lice. As a result, infected fish could always represent a subset of the population more susceptible to parasitism. For example, such fish may have less-developed immune and epidermal systems, which may facilitate preferential louse attachment and retention (Jones et al. 2008*a*). If infected fish are relatively underdeveloped physiologically, hypo-osmoregulatory ability might also lag behind the population mean, thus potentially explaining the observed reduction in gill NKA activity. Experiments that sample those fish that reject parasites or resist initial infection would help clarify this issue, while providing further insight into the mechanisms underlying host susceptibility.

Although infected OC and RC fish overlapped in terms of body mass, and a louse-associated ionic load tended to decrease with increasing fish mass in both groups, a plausible explanation for the absence of significantly elevated total body $[\mathrm{Na}^+]$ in naturally infected OC fish (>0.5 g) is that fish with a louse-related ionic load simply fail to survive in the wild. This possibility cannot be discounted. OC control fish could have also been previously infected in the wild, resulting in an altered ionic status equal to infected OC fish. The latter possibility, however, can likely be discounted for two reasons. First, epidermal damage was not observed in OC control fish, and second, total body $[\mathrm{Na}^+]$ and gill NKA activity were similar to size-matched control fish in the other experiments. Pathogens and other nonlouse factors in the Broughton Archipelago could also be contributing to a sampling bias within the OC fish population. Further laboratory infections with bigger fish (>0.5 g) and more advanced louse stages in a controlled setting should help clarify this issue. Unfortunately, high rates of louse loss and low sea louse availability will remain challenges for controlled infection studies.

This study provides some of the first sublethal measures of physiological impact by sea lice on juvenile pink salmon in both a controlled laboratory setting and the wild. We clearly show that body mass and hypo-osmoregulatory development are important in tolerating the effects of sea louse parasitism. Furthermore, sublethal hydromineral disruption is shown to occur in fish less than 0.5 g infected with one attached-stage louse. This size threshold for sublethal louse effects is also consistent with that for swimming performance (0.7 g; Nendick et al. 2011) and infection resistance mechanisms (immunocompetence and epidermis; 0.5–0.7 g; Jones et al. 2008*a*). We hope that management groups will take this information into consideration when making decisions concerning the interaction between sea lice and juvenile pink salmon. We also recommend that these data be further integrated with surrogate measures of ecological fitness before more definitive conclusions regarding wild fish survival are made. Despite the strength of the observations made here, the consequences of louse infection in the wild remain difficult to quantify with any certainty.

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Effects of flow fluctuations on habitat use and survival of age-0 rainbow trout (*Oncorhynchus mykiss*) in a large, regulated river[1]

Josh Korman, Carl Walters, S.J.D. Martell, W.E. Pine III, and Andrew Dutterer

Abstract: We evaluated effects of reduced hourly variation in flow from Glen Canyon Dam on survival of age-0 rainbow trout (*Oncorhynchus mykiss*) in the Colorado River, Arizona, USA, based on monthly abundance estimates. The proportion of the age-0 population in low-angle shorelines, which are potentially more sensitive to flow variability, declined from 70% in June to 20% in November as fish grew and made an ontogenetic habitat shift to deeper habitat. Average daily instantaneous mortality between August and September was 0.008 units lower in years when there was no change in the minimum flow compared with years when there was a sudden 50% reduction in the minimum flow. However, mortality was 0.006 units higher during the fall when there was no hourly variation in flow compared with years when flows fluctuated. As a result of these opposing patterns, 3-month age-0 survival across steady (0.31) and unsteady (0.28) flow regimes were very similar. While additional replication is required to strengthen inferences about effects of steadier flows, we demonstrate the utility of early life history monitoring for evaluating effects of flow management on fish populations in regulated rivers.

Résumé : Nous évaluons les effets d'une réduction de la variation horaire du débit provenant du barrage de Glen Canyon sur la survie des truites arc-en-ciel (*Oncorhynchus mykiss*) d'âge 0 dans le Colorado, Arizona, É.-U., d'après les estimations mensuelles d'abondance. La proportion de la population d'âge 0 sur les berges à pente faible, qui est potentiellement plus sensible à la variabilité du débit, a décliné de 70 % en juin à 20 % en novembre à mesure que les poissons ont grandi et ont fait un changement ontogénique d'habitat vers les eaux plus profondes. La mortalité instantanée journalière moyenne entre août et septembre est de 0,008 unités plus faible, les années durant lesquelles il n'y a pas de changement dans le débit minimum, par comparaison aux années durant lesquelles il y a une réduction soudaine de 50 % du minimum. Cependant, la mortalité est de 0,006 unités plus élevée durant l'automne lorsqu'il n'y a pas de variation horaire du débit, par comparaison aux années durant lesquelles les débits fluctuent. À cause de ces patrons opposés, la survie durant 3 mois des poissons d'âge 0 est très semblable dans les régimes de débits stables (0,31) et instables (0,28). Bien qu'il soit nécessaire de répéter ces expériences pour obtenir des conclusions plus solides sur les effets des débits plus réguliers, nous avons démontré l'importance de surveiller les premiers stades de vie lorsqu'on évalue les effets de la gestion des débits sur les populations de poissons dans les rivières à débit régulé.

[Traduit par la Rédaction]

Introduction

Hydroelectric dams alter the magnitude and frequency of flows and can have negative impacts on downstream fish communities (Cushman 1985). In some regulated rivers, power load following operations, often referred to as hydropeaking, result in considerable hourly variation in flow, depth, and water velocity, creating a highly variable physical environment. This impact is of special concern for juvenile fish, which in large rivers rear almost exclusively in shallow shoreline habitats (Gaudin 2001) that are destabilized by hydropeaking operations (Freeman et al. 2001). Hourly variation in flow can strand juvenile fish (Bradford 1997; Saltveit et al. 2001; Halleraker et al. 2003) and reduce their growth (Korman and Campana 2009) and is hypothesized to limit survival rates via indirect effects such as displacement out of preferred habitats; food depletion; and increases in stress, energetic costs, and predation risk (Scruton et al. 2003).

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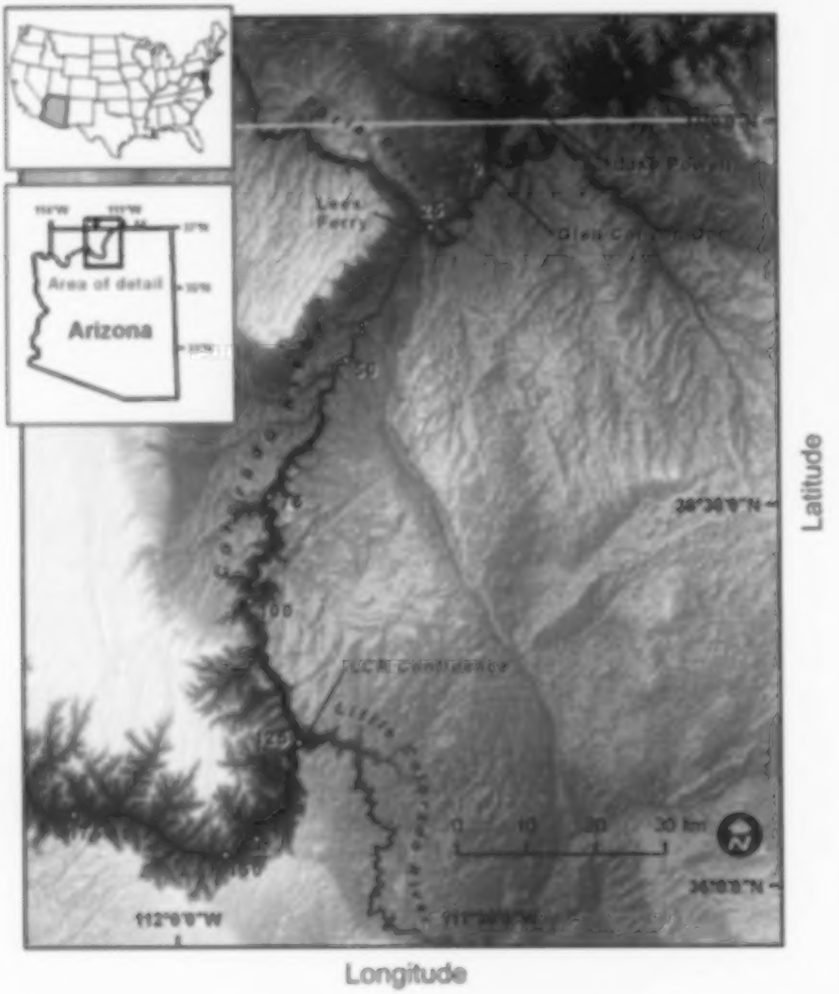
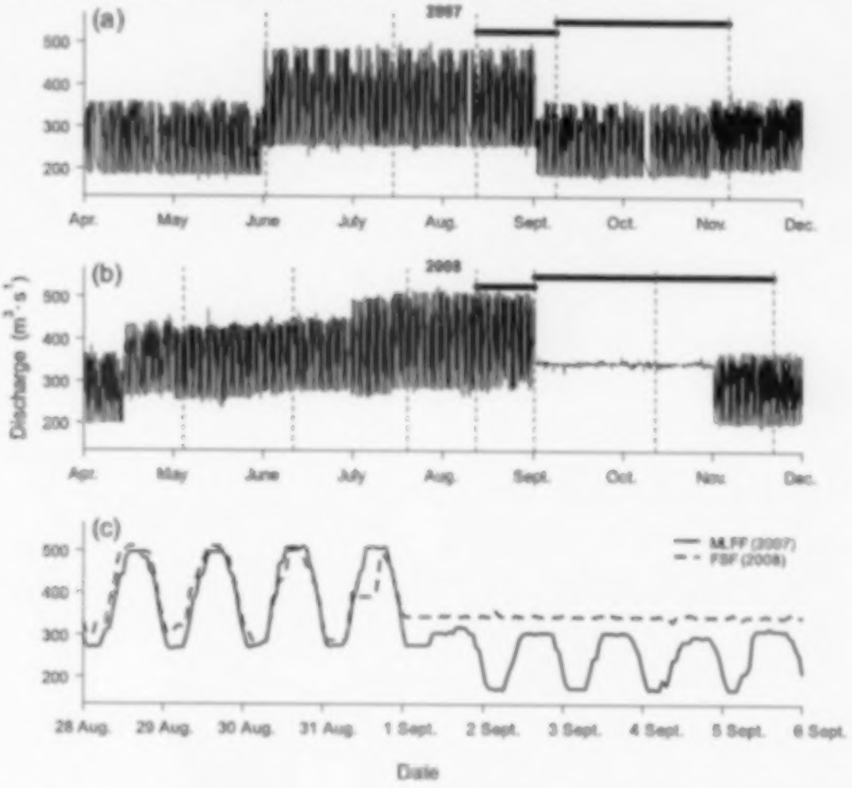
Fig. 1. Map of the study area (upper inset shows location of Arizona in USA, lower inset shows study location in Arizona). The Lees Ferry reach is a 26 km tailwater segment of the Colorado River between Glen Canyon Dam and Lees Ferry. Numbers beside the Colorado mainstem indicate river-kilometres downstream from the dam.



Humpback chub (*Gila cypha*) is a native fish endemic to the Colorado River that was listed as endangered in 1967 and is still considered endangered today (US Fish and Wildlife Service 2008). The largest population of humpback chub lives in the Colorado River in Grand Canyon near the confluence of the Little Colorado River (LCR) (Fig. 1). A major premise of the jeopardy opinion (US Fish and Wildlife Service 1978) is that hourly variation in flow from Glen Canyon Dam has been instrumental in causing the decline in the Grand Canyon population. In 1991, a modified low fluctuating flow (MLFF) regime was implemented to reduce the extent of hourly variation to improve the status of humpback chub and other native fishes. Although the chub population continued to decline for more than a decade after implementation of MLFF, the abundance of nonnative rainbow trout (*Oncorhynchus mykiss*) in the Lees Ferry reach, a 26 km tailwater located immediately below the dam (Fig. 1), increased by threefold (McKinney et al. 2001). Rainbow trout abundance in the mainstem Colorado River near the LCR increased by fivefold over this same time period (Makinster et al. 2010). This latter response was considered detrimental to humpback chub and other native fishes because of increased competition and predation (Gloss and Coggins 2005; Yard et al. 2011), so much so that a large-scale mechanical removal effort targeting rainbow trout was conducted between 2003 and 2006 (Coggins 2008).

In response to continued depressed abundance of humpback chub below Glen Canyon Dam, a new biological opinion was issued in 2008 (US Fish and Wildlife Service 2008), which called for a continuation of mechanical removal of trout near the LCR and implementation of steadier flows. This experimental regime, termed fall steady flows (FSF), eliminated hourly variation in flow during September and October (Fig. 2) when many juvenile chub disperse into the mainstem Colorado River from spawning and nursery areas in the LCR. However, considering the positive response of

Fig. 2. Hourly discharge from Glen Canyon Dam between April and December in 2007 under the modified low fluctuating flow (MLFF) regime (*a*) and in 2008 under the fall steady flow (FSF) regime (*b*). Flows over a 9-day period during the August to September minimum flow transition period under these two regimes are compared in panel (*c*). In all 6 study years, flows were higher and more variable in summer and lower and less variable in fall. The FSF regime eliminated the rapid reduction in the minimum flow on 1 September and hourly variation in flow in September and October. The vertical dashed lines in panels (*a*) and (*b*) show the date on the middle of each 5-day trip to sample age-0 trout. The thick solid lines at the top of panels (*a*) and (*b*) denote the periods when survival during flow transition and fall periods were measured. Hydrographs from other study years are not shown for brevity.



rainbow trout to steadier flows under MLFF, it is possible that the FSF regime could have a negative effect on humpback chub by increasing competition and predation. Understanding the response of early life stages of rainbow trout in the Lees Ferry reach to the FSF regime is important because (*i*) variation in recruitment strength and abundance of trout in Lees Ferry is likely determined by variation in survival rates of age-0 fish (e.g., Elliott 1994; Lobón-Cerviá 2005; Korman et al. 2011*a*); and (*ii*) trout abundance near the confluence with the LCR is largely controlled by emigration from the Lees Ferry reach (Coggins 2008).

The main objective of this study is to evaluate whether survival rates of age-0 rainbow trout in the Lees Ferry reach are affected by reduced flow fluctuations under the FSF regime and to gain understanding of the mechanisms driving a potential survival response. We examined seasonal and interannual trends in habitat use, growth, abundance, and survival of age-0 rainbow trout. Under the MLFF regime, the daily minimum flow was reduced by approximately 50% over 1 day between August and September, but under the FSF regime, there was only a negligible change in the minimum flow over this period (Fig. 2*c*). We hypothesized that the abrupt transition to lower flows under MLFF would result in lower survival between August and September relative to survival over this period under the FSF regime. We also hypothesized that age-0 rainbow trout survival rates would increase in September and October under the FSF regime because flows were stable. Assuming the abundance of age-0 rainbow trout prior to flow changes (late August) was similar across flow treatments, we would expect higher abundance by late fall (November) in years when FSF was implemented because of higher survival during transition and fall periods (Fig. 2).

Ontogenetic habitat shifts can effect survival of young fish (Biro et al. 2003; Werner and Hall 1988), and we interpret changes in age-0 trout survival to steadier flows in the context of size-related changes in habitat use. Impacts of hydropeaking on juvenile fish have been shown to vary by habitat type (Bain et al. 1988; Freeman et al. 2001; Shea and Peterson 2007). In the Lees Ferry reach, hydropeaking results in increased flows during the day and reduced flows at night (Fig. 2*c*), resulting in a diel lateral migration of immediate shoreline areas preferred by small fish. Surprisingly, most age-0 trout in this system hold further from shore in the per-

Table 1. Physical characteristics of sites sampled for age-0 rainbow trout in the Lees Ferry reach in 2004 (n = 20 for both low- and high-angle habitats).

	Low-angle		High-angle	
	August	September	August	September
Gradient (%)	12 (3)	—	37 (18)	—
Depth (cm)	31 (8)	18 (8)	61 (29)	64 (30)
Velocity (cm·s^{-1})	4.9 (8.0)	0.8 (2.4)	7.5 (11.2)	2.0 (3.8)

Note: Statistics show the average and standard deviation (in parentheses) of cross-sectional gradient (i.e., gradient of shoreline perpendicular to direction of flow) and water depth and average velocity at 1.5 m from the shoreline. Measurements were taken at the daily minimum flow when fish sampling was conducted, which was 285 and 142 m^3·s^{-1} in August and September, respectively. See Korman and Campana (2009) for details of the methods used to collect these data.

manently submerged zone, rather than migrate up and down the fluctuating shoreline (Korman and Campana 2009). Diel changes in flow result in greater variation in depth and velocity over the permanently submerged zones used by age-0 rainbow trout in lower-angle shorelines such as cobble bars than in higher-angle shorelines such as talus slopes. As well, a change in the minimum flow will result in greater horizontal displacement of the permanently submerged zone in low-angle shorelines. Owing to these factors, we hypothesized that effects of diel variation in flow and changes in the minimum flow on energetics and predation risk for age-0 trout will be greater in low- than in high-angle shorelines. Thus, the overall response of the age-0 population to changes in the minimum flow and steadier flows will depend on the extent of overlap in the timing of use of low- and high-angle shorelines in relation to the timing of changes in flow variability. Survival responses to changes in flow should be more pronounced when there is greater utilization of more flow-sensitive, low-angle shorelines.

In this paper, we use relatively simple analyses to examine patterns of habitat use, growth, and survival of age-0 rainbow trout in a regulated river. In a companion paper, we demonstrate that this information can be integrated into a stock synthesis model as a more sophisticated quantitative framework for understanding early life history dynamics (Korman et al. 2011*b*).

Materials and methods

To evaluate whether changes in flow regime affected survival rates of age-0 rainbow trout in the Lees Ferry reach (Fig. 1), we estimated reach-wide abundance on a near-monthly basis from spring through fall over 6 years between 2004 and 2010 (no data were collected in 2005). Apparent daily instantaneous mortality rates were computed based on the ratio of abundances over adjacent sampling trips. The effect of MLFF and FSF regimes (Fig. 2) on age-0 survival was evaluated by examining differences in mortality estimates between regimes during the August to September flow transition period and in the fall (September to November). We compared seasonal trends in abundance and length frequencies in low- and high-angle shorelines to describe variation in habitat use to help interpret differences in mortality rates between flow regimes. Determination of daily age from hatch from otolith microstructure was used to estimate length-at-age relationships in each habitat type, which in turn were used to interpret size-related patterns of habitat use and evidence for an ontogenetic habitat shift.

Study site and experimental flow treatments

The Lees Ferry reach of the Colorado River begins at Glen Canyon Dam and extends 26 km downstream to the confluence with the Paria River (Fig. 1). Because of clear and cool tailwater habitat below the dam, the fish fauna in the Lees Ferry reach is almost exclusively nonnative rainbow trout (McKinney et al. 2001). The majority of rainbow trout spawn between February and April, and emergence occurs approximately 2 months after fertilization (Korman et al. 2011*a*). The reach is wide, shallow, and low-gradient, with water temperatures and secchi depths typically in the range of 9–12 °C and 6–7 m, respectively (Voichick and Wright 2007). Average discharge (USGS gage 09380000) in study years (2004–2010, excluding 2005) was 332 m^3·s^{-1}, and average wetted width, depth, and water surface gradient was 142 m, 5.2 m, and 0.025% (0.25 m·km^{-1}), respectively (Randle and Pemberton 1987).

Discharge from Glen Canyon Dam fluctuates on a diel cycle that is driven by power demand, but controlled through a suite of operating rules that define the current MLFF operating regime. These rules constrain the maximum daily flow range, minimum and maximum flows, and hourly ramping rates. During summer months when power demand is high (July and August), flows within a day typically range from 260 to 490 m^3·s^{-1} (Fig. 2). This range in summer flows occurred in all study years because the FSF regime only affected flows after August. In fall months (September and October) under normal operations (MLFF 2004–2007), diel variation in flow (170–320 m^3·s^{-1}) was lower than that in summer and was effectively eliminated under the FSF regime (FSF 2008–2010, 295–300 m^3·s^{-1}).

Age-0 abundance, habitat use, and apparent mortality rate

Age-0 rainbow trout were captured by backpack and boat electrofishing in low- and high-angle shorelines, respectively. High-angle shorelines were composed of large and angular sandstone boulders (talus) with large interstitial spaces and were typically associated with outside river bends. Low-angle shorelines were mostly composed of cobble and clean sand substrate on depositional bars associated with inside river bends and eddy complexes. Between the daily minimum and maximum flows during summer months, average shoreline gradients (perpendicular to direction of flow, Table 1) re-

Table 2. Summary of effort and sample sizes used to monitor age-0 abundance and length-at-age in the Lees Ferry reach.

Year	No. of survey trips	Survey period	Total catch	No. of fish aged
2004	7	Apr.–Nov.	4 360	318
2006	5	June[a]–Nov.	1 834	137
2007	5	June–Nov.	5 216	152
2008	7	May–Nov.	12 059	100
2009	6	May–Nov.	12 686	101
2010	4	July–Nov.	4 315	0

Note: No data were collected for brood year 2005.

[a] Only low-angle habitat surveyed on June trip in 2006.

sulted in a diel lateral shift in the shoreline of 6.5 and 2.2 m in low- and high-angle shorelines, respectively (Korman and Campana 2009). Depth in high-angle shorelines was twofold greater than in low-angle ones. Under the MLFF regime, depth was reduced by approximately 50% in low-angle shorelines between August and September because of the reduction in flow, but little change occurred in high-angle shorelines. Velocity in all shoreline habitats was generally slow owing to the low gradient of the reach and was even slower after August when flows were reduced.

Sampling trips were conducted on a near-monthly basis, typically from May through November (Fig. 2; Table 2). On each trip, approximately 2.5% and 4.5% of the total low- and high-angle shoreline length in the Lees Ferry reach was sampled, respectively. All sampling was conducted at night at minimum flow to maximize capture probability (Korman and Campana 2009). Population estimates were determined using a random-stratified design. A total of 20 habitat units were randomly selected from a spatially referenced shoreline habitat database from both low- and high-angle habitats (Mietz 2003). Within those units, random 30 m shoreline lengths were sampled on each trip using single-pass backpack electrofishing in low-angle shorelines. Random 50 m shoreline lengths from the 20 sites in high-angle habitat were sampled using single-pass boat electrofishing (see Korman et al. 2009 for sampling details). After electrofishing each site, fish were anesthetized and fork lengths were measured to the nearest milimetre. A subsample of three to five fish within 10 mm length categories between 20 and 100 mm across the 40 sites sampled each trip were sacrificed and preserved in 95% ethanol to determine daily age from hatch and emergence based on otolith microstructure (Table 2).

Age-0 abundance on each sampling trip was estimated using a two-stage design. Abundance at each sampling site was calculated by dividing catch by capture probability determined from mark–recapture experiments conducted in 2007 and 2008 (Korman et al. 2009). An estimate of abundance for the reach was then obtained by dividing the sum of population abundances across sites by the proportion of shoreline habitat that was sampled relative to the total for the reach. The approach is similar to the method used by Mitro and Zale (2000) to estimate age-0 trout abundance in the Henrys Fork of the Snake River. They allowed capture probabilities to vary across trips and used a mean capture probability for all size classes. We allow capture probability to vary with fish size and assume this relationship does not vary across trips (Korman et al. 2009).

The population size at each single-pass electrofishing site sampled in the first stage was determined from

$$(1)\qquad n_{t,h,i}=\sum_{j=1}^{31}\frac{c_{t,h,i,j}}{p_{h,j}}$$

where $n_{t,h,i}$ is the population estimate on sampling trip t for site i in habitat type h, $c_{t,h,i,j}$ is the catch in size category j (20–170 mm in 5 mm increments), and $p_{h,j}$ is the habitat-specific, size-dependent capture probability calculated from a logistic function whose parameters were estimated from mark–recapture data (Korman et al. 2009). The total population size in each habitat type for the entire Lees Ferry reach was then calculated from

$$(2)\qquad N_{t,h}=\frac{\sum_{i} n_{t,h,i}}{\left(\dfrac{\sum_{i}\mathrm{SL}_{t,h,i}}{\mathrm{SL}_{h}}\right)}$$

where $N_{t,h}$ is the total population size on sampling trip t in habitat type h, $\mathrm{SL}_{t,h,i}$ is the shoreline length of each sample site, and SL_h is the total length of shoreline of that habitat type in the reach. The denominator in eq. 2 represents the proportion of shoreline sampled on each trip, which was typically 0.022 (20 sites·reach^{-1} × 30 m·site^{-1} / 27 800 m·reach^{-1}) and 0.047 (20 sites·reach^{-1} × 50 m·site^{-1} / 21 500 m·reach^{-1}) for low- and high-angle shorelines, respectively. Reach-wide age-0 population estimates (N_t) were calculated as the sum of estimates in low- and high-angle habitat types.

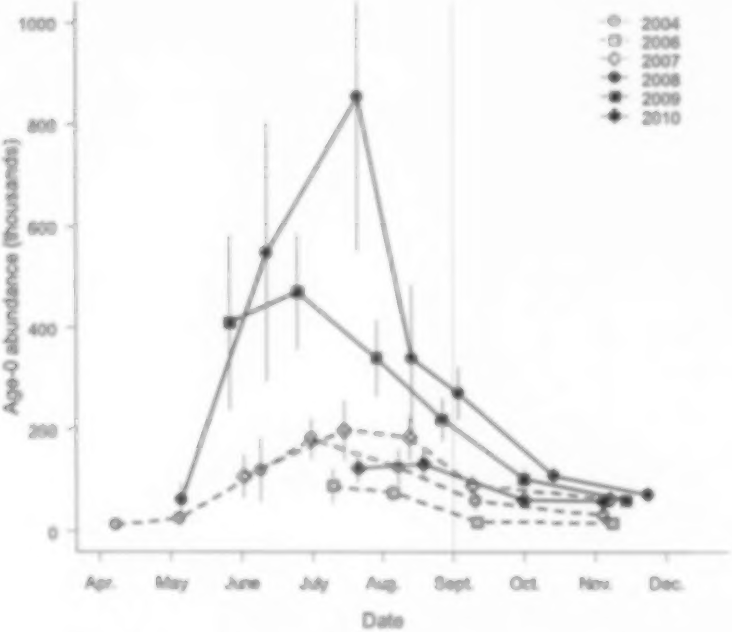
Seasonal variation in habitat use was described by comparing temporal trends in reach-wide abundance in low- and high-angle habitat types ($N_{t,h}$ from eq. 2). To construct length–frequency distributions for a given habitat type and sampling trip, corrected for size-dependent differences in capture probability, we computed $n_{t,h,i,j}$ as an intermediate step in eq. 2, summed estimates across sites to determine $n_{t,h,j}$, and then computed the proportions in each size class as the ratio of $n_{t,h,j}$ to the sum of the population estimates across size classes ($n_{t,h}$).

Daily instantaneous apparent mortality rates (M) were computed from

$$(3)\qquad M_{t_1}=\frac{-\log\left(\frac{N_{t_2}}{N_{t_1}}\right)}{t_2-t_1}$$

where N_t is the reach-wide age-0 abundance estimate on Julian days t_1 and t_2, the Julian dates of the middle of each sampling trip. M therefore represents the daily apparent mortality rate between two adjacent trips. We use the term "apparent mortality" because the calculation is based solely on differences in abundance over time and does not account for recruitment into the age-0 population that is sampled or losses due to outmigration from the Lees Ferry reach. To integrate the effect of changes in mortality across the flow transition and fall periods, we computed a survival rate over a 3-month interval (August to November) beginning 15 August. We first computed a time-weighted average daily mortality rate over this period (M_{avg}) based on mortality rates between

Fig. 3. Seasonal trends in the total abundance of age-0 rainbow trout in the Lees Ferry reach by year between 2004 and 2010 (no data collected in 2005). Error bars denote the 95% confidence intervals for abundance estimates. Gray- and black-filled symbols denote years when the modified low fluctuation flow (MLFF) and fall steady flow (FSF) regimes were implemented, respectively. Note that differences in flow in years when MLFF (2004–2007) and FSF (2008–2010) regimes were implemented only occurred after 31 August, highlighted by the vertical dashed line.



August to September and September to November sampling trips (i.e., $M_{avg} = (M_{Aug.-Sept.} + 2M_{Sept.-Nov.})/3$) and then converted this daily mortality rate to a 3-month survival rate (i.e., $S = \exp(-90M_{avg})$).

Uncertainty in abundance estimates was determined using a nonparametric bootstrap procedure. For each bootstrap trial, 20 sample sites from each habitat strata for each sampling trip were randomly drawn with replacement. Catches from the selected sites were converted to population estimates using eq. 1, which in turn were converted to a reach-wide estimate of abundance by summing the habitat-specific abundance values determined from eq. 2. The mean and 95% confidence interval of the distribution of abundance estimates, which was computed based on values from all trials, was used to characterize the expectation and uncertainty in trip-specific abundance.

The expected value and probability distribution of mortality rates under MLLF (2004–2007) and FSF (2008–2010) regimes for the August to September and September to November periods were computed by randomly sampling from bootstrapped estimates of abundance across years associated with each of these regimes. The approach accounts for uncertainty in both year-specific estimates of mortality and variation in mortality across years within treatments. On each trial, mortality rates for each of three randomly selected years under MLFF and FSF regimes were computed from eq. 3 and averaged to represent the expected value for the MLFF or FSF regimes. Bootstrapped mortality estimates were also used to estimate the probability distribution of the time-integrated survival rate from August to November. 200 000 bootstrap samples were required to produce stable estimates of the expected values and confidence intervals.

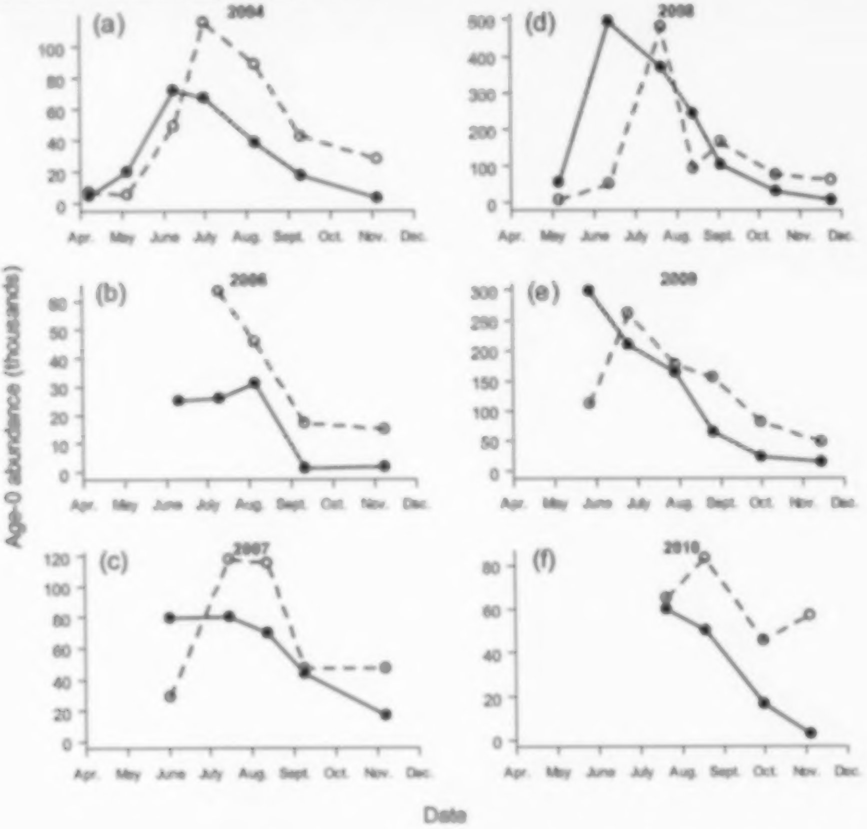
Statistical evaluation of flow regime effects

We used a confidence interval approach to compare the effects of flow regime on mortality rates (Steidl et al. 1997). The appropriateness of the standard hypothesis-testing framework in ecological studies has been the subject of lively debate (see review in Bradford et al. 2005). A key issue in this debate is the distinction between statistical significance and the affirmation of an effect of biological importance. The rejection of the null hypothesis provides no direct evidence of the magnitude of the estimated effect or its precision. In this analysis, we compuied probability distributions of differences in mortality rates between flow regimes, for both August to September and September to November periods, based on the bootstrapped mortality rates described above. To determine whether differences in the integrated 3-month survival rate effected recruitment to the adult population, we compared distributions of age-0 abundance estimates in August, prior to any flow changes, and in late fall sample (November) in MLFF and FSF years.

Habitat and year effects on age-0 length-at-age and growth

As part of the evaluation of an ontogenetic shift in habitat use from low- to high-angle shorelines, we tested whether length-at-age for age-0 trout differed between habitat types and years. Daily age of trout from hatch to the date of capture was determined from otolith microstructure. Both sagit-

Fig. 4. Comparisons of seasonal trends in age-0 rainbow trout abundance in all low-angle (solid line and filled circles) and high-angle (dashed line and open circles) habitat in the Lees Ferry reach, 2004–2010.



tal otoliths were removed from preserved fish and mounted individually on microscope slides in cyanoacrylate glue. Otoliths were polished close to the midplane, flipped and reglued, then polished to the growth plane with 30 and 3 μm lapping film, as per established procedures (Stevenson and Campana 1992). All otoliths were examined at a magnification of 400–1250× under a compound microscope. Using the well-defined hatch and emergence checks as reference points, daily increments between the checks and edge were counted two to four times in at least one otolith of each pair (Campana 1992). The average counts were recorded as the age from hatch and emergence to capture. Ageing was not conducted in 2010 because of funding limitations.

Length-at-age relationships were estimated assuming that observation error was log-normally distributed around linearly increasing mean length with age:

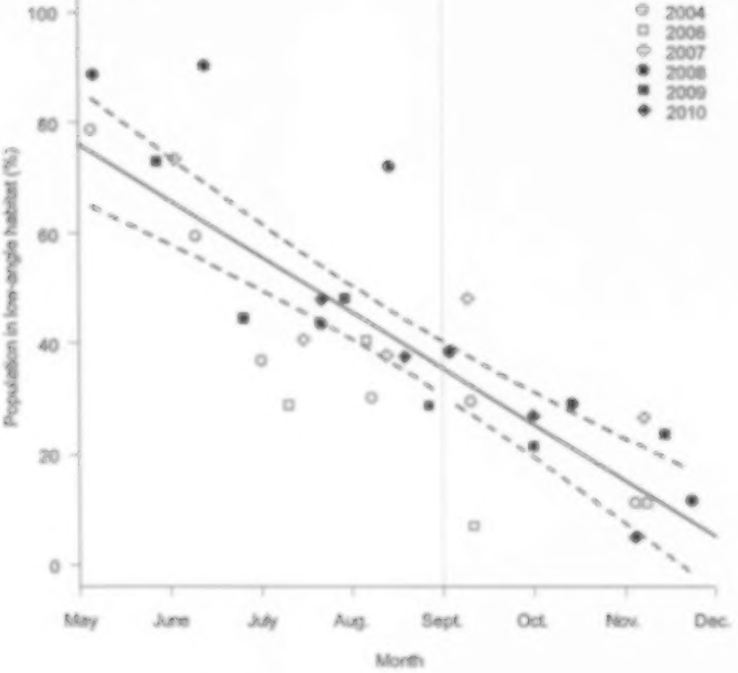
$$(4) \qquad L = (\alpha_0 + \alpha_1 A)\exp(v)$$

where L is fork length (mm), A is age (days from hatch), α_0 and α_1 are the intercept (size-at-hatch in mm) and slope (average growth rate among individuals in mm·day^{-1}), respectively, and v is a random deviate from a normal distribution with a mean of 0 and a standard deviation σ. Sample sizes used to estimate length-at-age relationships are provided in Table 2. Length-at-age models were fit to the data by maximum likelihood estimation using Solver in Excel. We estimated parameters for a global model where all parameters (α_0, α_1, and σ) could vary for each combination of habitat type and year. We also estimated parameters from simpler models where parameters could vary only by year, only by habitat type, or were constant across all year–habitat strata (null model). We used the Akaikie information criteria corrected for small sample size (AIC$_c$) to compare models (Burnham and Anderson 2002). Models with AIC$_c$ values that are similar to the model with the lowest AIC$_c$ score were considered to have strong support (ΔAIC$_c$ = 0–2), while those with larger AIC$_c$ values were considered to have moderate (ΔAIC$_c$ = 4–7) or essentially no (ΔAIC$_c$ >10) support.

Results

Abundance of age-0 trout increased in spring as fish emerged from the gravel and began recruiting to the sampled population at a minimum size of 20–25 mm (Fig. 3). Abundance peaked by mid-July and then began declining because of reduced recruitment and cumulative effects of mortality. Age-0 trout occupied primarily low-angle shorelines in May to June and increased their use of high-angle shorelines over the summer (Fig. 4). The proportion of the total age-0 population in low-angle habitat declined by 10%·month^{-1} between

Fig. 5. The percentage of the Lees Ferry age-0 trout population in low-angle habitat between May and December 2004–2010. Gray- and black-filled symbols denote years when modified low fluctuating flow (MLFF) and fall steady flow (FSF) regimes were implemented, respectively. The solid and dashed lines represent the mean relationship estimated using data from all years and the 95% confidence limits, respectively. Note that differences in flow in years when MLFF (2004–2007) and FSF (2008–2010) were implemented only occurred after 31 August, highlighted by the vertical dashed line.

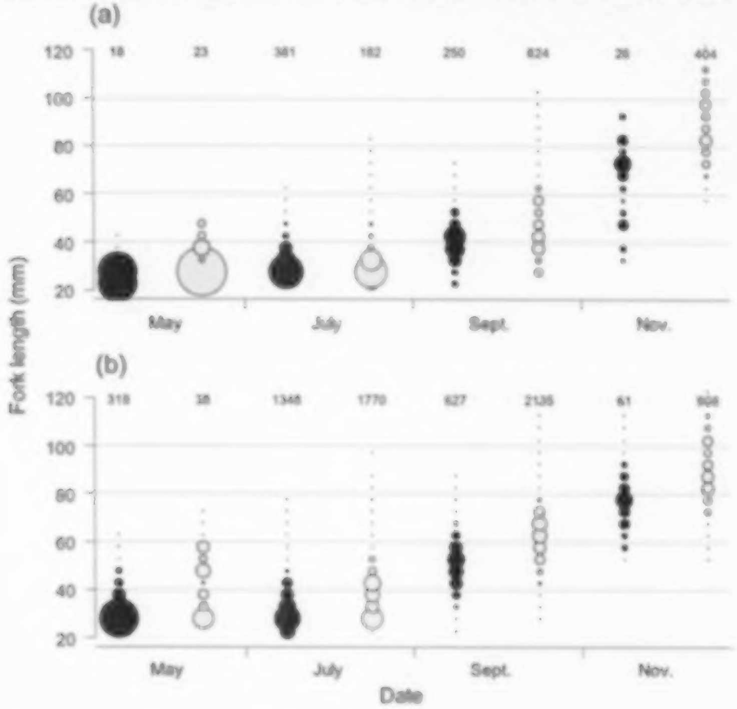


May and November, and the slope of this relationship was significantly different than zero ($F_{[1,30]} = 69.2$, $p < 0.001$, $r^2 = 0.70$; Fig. 5). There was no indication that this pattern was different in months affected by the FSF regime. Age-0 trout between 25 and 40 mm were the dominant size classes in both habitat types in May through July, indicating that some recently emerged trout recruited directly to high-angle shorelines (Fig. 6). As the season progressed, fish grew and the length–frequency distributions shifted upwards. Within sampling trips, larger fish were more common in high-angle shorelines and this difference increased through the growing season. The slope of a linear regression between Julian day and the difference in mean lengths between high- and low-angle shorelines within trips was positive and significantly different than zero ($F_{[1,31]} = 9.73$, $p = 0.004$, $r^2 = 0.24$).

There were strong linear relationships between daily age from hatch and fork length, indicating that growth rates were relatively constant for trout between 25 and 100 mm (Fig. 7). Age predicted 80%–93% of the variation in length among individuals based on the global model where the constant (size-at-hatch), slope (growth rate), and variance parameters could vary by year and habitat type (Table 3*a*). The average growth rate across all strata was 13 mm·month^{-1}. The low coefficient of variation in length-at-age ($\sigma = 0.09$–0.14) indicated that at least 50% of the variation in fish size within habitat-stratified samples (Fig. 6) was driven by variation in hatch timing, with the remaining variation driven by differences in growth rates among individuals. There was much more variation in length-at-age across years than across habitat types. The year-specific length-at-age model was the most parsimonious (i.e., lowest AIC$_c$) of the four candidate models that were considered (Table 3*b*). There was no support for the null and habitat-specific models and moderate to no support for the global model that allowed parameters to vary by year and habitat type. The limited support for models that included habitat effects occurred because there were very small differences in length-at-age between habitat types within years (0–7 mm at 180 days from hatch; Table 3*a*; Fig. 7).

Daily mortality during the August to September flow transition was on average sevenfold higher than mortality between September to November in years with a 50% reduction in the daily minimum flow (MLFF) on 1 September, but only twofold higher in years when this flow reduction was eliminated (FSF; Fig. 8*a*). The daily mortality rate under FSF during the August to September period, when the abrupt flow transition was eliminated, was less than the mortality rate under MLFF (mean $\Delta \sim -0.008$), while the converse was true under steady flows during the September to November period (mean $\Delta \sim 0.006$; Fig. 8*b*). As a result of these opposite responses, the expected 3-month survival rates from August to November under both regimes were similar (MLFF = 0.31, FSF = 0.28; Fig. 8*c*). Mean age-0 abundance in November in years when FSF was implemented (64 800) was 1.7-fold higher than the mean in years when MLFF was implemented (37 700). This difference was substantive, as 95% confidence intervals for MLFF (31 600–43 800) and

Fig. 6. Length–frequency distributions of age-0 trout, corrected for size-dependent capture probability, for a subset of months and by habitat type in 2004 (*a*) and 2008 (*b*). Black- and gray-filled circles denote low- and high-angle habitat, respectively. The diameter of the circles is proportional to the ratio of fish caught by size class to the total fish caught within each month–habitat stratum (column). Numbers at the top of each column denote the total catch by stratum. Length–frequency distributions for other months and years are not shown for brevity.



FSF (58 500–71 200) means did not overlap. However, the difference was not related to the FSF regime because August age-0 abundance in 2 of the 3 FSF years (2008 and 2009), prior to implementation of the flow change, was substantially higher than that in years under MLFF (Fig. 3).

Discussion

We hypothesized that stabilized flow from Glen Canyon Dam would decrease mortality and increase abundance of age-0 rainbow trout in the Lees Ferry reach. Daily instantaneous mortality rates between August and September were lower in years when there was no change in the minimum flow (FSF) on 1 September compared with years when there was a sudden reduction in the minimum (MLFF), but mortality rates were higher in the fall (September to November) when flows were steady (FSF). The integrated survival rate from late summer through fall was very similar across flow regimes (MLFF = 0.31, FSF = 0.28) because of these opposing mortality responses. Inferences about the effects of steadier flows are complicated by low replication within treatments and potential differences in density-dependent mortality between treatments. Density-dependent fall mortality under FSF may have been higher, because abundance in 2 of 3 study years, prior to the start of steady flows, was approximately twofold greater relative to MLFF, and this may have overwhelmed potential increases in survival due to steady flows. Mortality over the minimum flow transition pe-

Fig. 7. Length-at-age relationships for age-0 rainbow trout in the Lees Ferry reach in 2007 based on counts of daily otolith rings. Closed and open circles denote fish collected in low- and high-angle habitats, respectively. Solid and dashed lines are the best-fit relationships in low- and high-angle habitats, respectively. Relationships for other years are not shown for brevity (see Table 3*a* for parameter estimates).

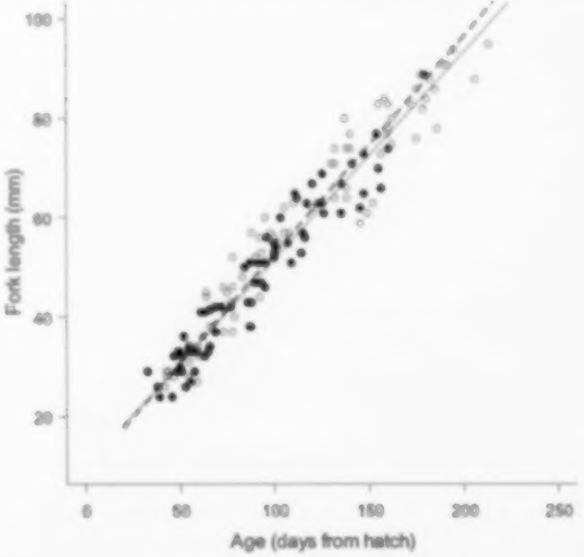
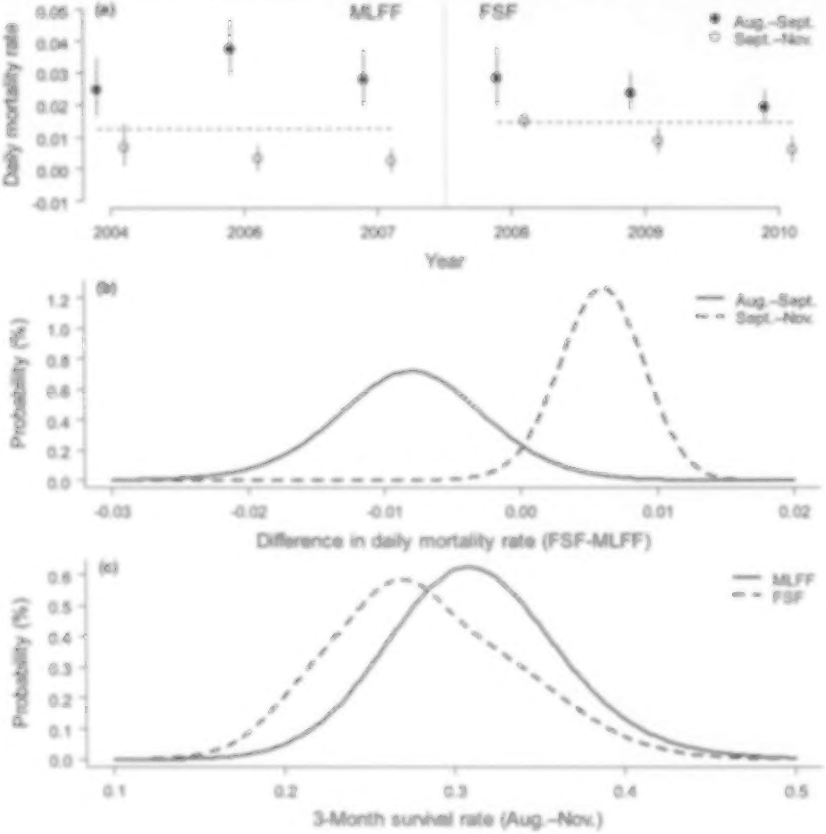


Fig. 8. Daily instantaneous mortality rates and 3-month survival rates of age-0 rainbow trout in late summer and fall in the Lees Ferry reach across the 6 study years. Panel (*a*) shows the mean daily instantaneous mortality rates (points) and 95% confidence intervals (vertical lines) between August and September (filled circles) and September and November (open circles) in years under the modified low fluctuating flow (MLFF) and fall steady flow (FSF) regimes. The horizontal dashed lines show the average time-integrated daily mortality rate between August and November across years within each flow regime. Panel (*b*) shows probability distributions of the difference in daily mortality rates between flow regimes. Panel (*c*) shows probability distributions of the 3-month integrated survival rate under each flow regime.



riod (August to September) under FSF was lower than that under MLFF in spite of higher densities, suggesting a potentially strong flow effect in this case. Additional replication is needed to resolve these uncertainties.

We observed a strong seasonal- and size-dependent change in habitat use by age-0 rainbow trout, with the proportion of the total population in low-angle habitat declining steadily from late spring through fall. Prior to 1 September (when minimum flows were changed in MLFF years), approximately 40% of the age-0 population remained in low-angle habitat, which is potentially more sensitive to variation in flow than high-angle habitat. We speculate that higher mortality between August and September under MLFF compared with FSF occurred because a large proportion of the population was located in a potentially flow-sensitive habitat prior to the flow change. Conversely, most age-0 trout were found in potentially flow-insensitive, high-angle shorelines during fall months, and this may have limited the survival response to steady flows. This hypothesis is consistent with a number of studies that show hourly variation in discharge can cause greater destabilization in lower angle, shallow shoreline environments relative to steeper ones (Bain et al. 1988; Bowen et al. 1998; Shea and Peterson 2007).

Trends in length–frequency distributions and growth of age-0 trout provided additional insight into the low- to high-angle habitat shift. Age-0 trout were larger in high-angle shorelines than in low-angle ones, and this difference increased over the growing season. This pattern could indicate that (1) the proportion of fish moving from low- to high-angle shorelines increases with size, and there are limited differences in growth and size-dependent survival rates among habitat types; or (2) movement does not depend on size, and differences in length–frequency distributions between habitats are caused by faster growth in high-angle habitat (2*a*) or by a greater decline in survival with decreasing fish size in high-angle habitat (2*b*). Our data cannot distinguish between the size-dependent movement (1) and size-dependent survival (2*b*) hypotheses. However, the habitat-specific growth hypothesis (2*a*) is not well supported, as differences in length-at-age between habitat types were too small (0–7 mm at 180 days from hatch) to explain the larger differences in length–frequency distributions (10–15 mm by November). It

Table 3. Parameter estimates for (*a*) the global (year–habitat) length-at-age model and (*b*) comparison of alternate models based on the Akaikie information criteria corrected for small sample size (AIC_c).

(*a*) Global (year–habitat) length-at-age model.

Strata	α_0	α_1	σ	r^2	*n*	FL @ 180 days
2004–low	9.55	0.37	0.12	0.85	120	76
2004–high	8.26	0.41	0.15	0.78	198	83
2006–low	10.56	0.46	0.12	0.86	59	93
2006–high	10.23	0.46	0.12	0.87	77	93
2007–low	9.81	0.42	0.09	0.93	70	85
2007–high	8.91	0.44	0.10	0.93	82	87
2008–low	10.94	0.43	0.14	0.80	46	89
2008–high	12.00	0.43	0.13	0.80	54	89
2009–low	12.06	0.42	0.10	0.88	51	88
2009–high	7.72	0.47	0.11	0.83	50	92

(*b*) Comparison of alternate models.

Model	*K*	LL	AIC_c	ΔAIC_c
Null	3	446.9	–887.8	181.6
Year	15	550.0	–1069.4	0
Habitat	6	450	–887.0	182.4
Year–habitat	30	561.7	–1060.9	8.4

Note: Columns in (*a*) denote the most likely estimates of the intercept (α_0, size at hatch in mm), slope (α_1, growth rate in mm·day^{-1}), and standard deviation (σ in mm) of the linear length-at-age relationships; the coefficient of determination (r^2); sample size (*n*); and predicted fork length at 180 days from hatch (FL @ 180 days in mm). Columns in (*b*) denote the number of parameters that are estimated (*K*), log-likelihood (LL), and the difference in AIC_c values relative to the model with the lowest AIC_c value (ΔAIC_c).

is possible that we underestimated growth rates in high-angle habitat, as some fish that were sampled there may have migrated from low-angle habitat. However, as large numbers of 30–40 mm fish were already present in high-angle habitat by July, differences in growth between habitat types should have been evident in the length-at-age relationships, but were not.

The ontogenetic shift in age-0 habitat use in the Lees Ferry reach may have been caused by differences in predation risk and growth potential in low- and high-angle shoreline habitats. A shift between these habitat types could be considered analogous to a shift from riffles to pools in small streams (e.g., Chapman and Bjornn 1969) or from littoral to pelagic zones within lakes (e.g., Biro et al. 2003). Habitat shifts of young fish can be driven by differences in avian and piscivorous predation risk determined by water depth (Werner and Hall 1988; Power et al. 1989; Lonzarich and Quinn 1995). This would explain the habitat use pattern by age-0 trout in the Lees Ferry reach, where growing fish shifted from low- (shallow) to high- (deep) angle habitats as they became more vulnerable to birds and less vulnerable to piscivorous fish. Differences in growth potential between habitat types could also be driving the observed size-dependent variation in habitat use (e.g., Rosenfeld and Boss 2001). In the Lees Ferry reach, the utility of low-angle shorelines for age-0 trout may decline between summer and fall as energetic demands increase and may outstrip the growth potential of shallow habitat. Note that the habitat-specific length-at-age relationships cannot be used to evaluate growth potential differences because they integrate effects of food availability, predation risk, and fish density. Mesocosm studies that measure individual growth rates and can control these factors are needed to quantify these dynamics.

Some important factors were not represented in our estimation of age-0 mortality that could potentially lead to bias in these rates and how they changed with flow. These include (*i*) recruitment of newly emerged fish to the age-0 population; (*ii*) size-dependent effects on mortality; (*iii*) movement between habitat types; and (*iv*) outmigration from the study reach. The first three issues can be addressed by using a more sophisticated approach to estimate mortality rates (see Korman et al. 2011*b*). Average daily instantaneous mortality rates between August and November ranged from 0.005 to 0.04, which encompass age-0 mortality rates determined for Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and rainbow trout (Nislow et al. 2004, M = 0.01–0.02; Einum and Nislow 2005, M = 0.002–0.027; Berg and Jorgensen 1991, M = 0.007–0.032; Elliott 1994, M = 0.012; Hume and Parkinson 1988, M = 0.003–0.005). While this comparison suggests that large biases in our mortality estimates are unlikely, the range of published values is wide, making it difficult to determine if smaller biases exist. Substantial downstream migration of age-0 trout from the Lees Ferry reach during summer or fall would result in an overestimate of reach-wide mortality rates. However, this is unlikely as age-0 trout are rarely caught downstream (Korman et al. 2005; Coggins 2008).

Most assessments of experimental changes to habitat are based solely on monitoring adult populations or perhaps a single juvenile life stage. Results from this study highlight the risks of such an approach. A controlled flood from Glen Canyon Dam, conducted in March 2008, resulted in a 4.5-fold increase in early survival rates (fertilization to 1 month from emergence) of age-0 rainbow trout from the 2008 brood and a 2.5-fold survival increase from the 2009 brood (Korman et al. 2011*a*). In the comparison of MLFF and FSF regimes, we noted that the abundance of age-0 trout in late fall was on average twofold higher in years when the FSF regime was implemented. However, because we saw little effect of the FSF regime on the integrated survival rate from late summer through fall and observed higher age-0 abundance before the FSF regime in 2 of 3 years (i.e., prior to 1 September), it is clear that steadier flows were not the cause for the increase in fall abundance. In the absence of seasonal trends in abundance and survival presented here, the effects of the controlled flood and the steady flow regime would have been confounded, and higher age-0 abundance in fall could have been mistakenly attributed to the FSF treatment.

In adaptive management settings, poor understanding of critical mechanisms regulating population size make it very difficult to provide substantiated arguments in support of a particular flow experiment in the first place. This often results in an experimental design that is compromised by political, legal, and economic concerns, which limit the rate of learning about system response. Early life history studies can provide useful data to develop more informative experiments. In the case of the Glen Canyon Dam Adaptive Management Program, the 2008 biological opinion for humpback chub (US Fish and Wildlife Service 2008) calls for long-term implementation of an intensive mechanical removal effort targeting rainbow trout. This program will be costly and is strongly opposed by recreational users and the Hopi and Zuni tribes. As a result, there is much interest in determining if the removal effort can be curtailed by altering flows from the dam to control trout abundance. Relatively extreme hourly fluctuations in flow during the early operation of the dam (i.e., before 1991) were unintentionally very effective at limiting trout abundance (McKinney et al. 2001), but a return to such operations would have negative effects on recreational users and a number of physical and biological resources in Grand Canyon (Lovich and Melis 2007). However, a more limited fluctuating flow regime, targeting juvenile trout after the majority of density dependence has occurred, but before they leave habitats that are potentially more sensitive to flow fluctuations, may be effective. Information from this study suggests that it would be worth testing a regime where flow variation is increased during late spring and summer months when small age-0 trout are utilizing potentially flow-sensitive, low-angle habitat.

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Describing population dynamics for early life stages of rainbow trout (*Oncorhynchus mykiss*) using a stock synthesis model[1]

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Abstract: A stock synthesis model was used to assess effects of experimental flows on early life stages of nonnative rainbow trout (*Oncorhynchus mykiss*) in the Colorado River below Glen Canyon Dam (Arizona, USA). The model estimated time-varying survival rates while correcting for entry of new recruits to the age-0 population and changes in vulnerability to capture associated with growth and ontogenetic habitat shifts. A controlled flood, designed in part to enhance native fish habitat, led to an 11-fold increase in early survival rates (fertilization to ~1 month from emergence) of weekly cohorts of trout fertilized after the flood. Effects of increased flow fluctuations during incubation, designed to reduce trout abundance, were not apparent. Age-0 mortality between August and September was over twofold higher in years when there was a 50% reduction in the minimum flow compared with years when flow was stable. There was strong support for models that simulated an ontogenetic shift to deeper habitat in four of five study years. The integration of detailed field information in a stock synthesis model to describe early life history dynamics is a valuable approach that can be applied in a wide range of systems.

Résumé : Un modèle de stock synthèse nous a servi à évaluer les effets de débits expérimentaux sur les premiers stades de vie de truites arc-en-ciel (*Oncorhynchus mykiss*) non indigènes dans le Colorado en aval du barrage de Glen Canyon (Arizona, É.-U.). Le modèle estime les taux de survie qui varient en fonction du temps tout en tenant compte de l'arrivée de nouvelles recrues dans la population d'âge 0 et des changements dans la vulnérabilité à la capture associés à la croissance et aux changements ontogéniques d'habitat. Une crue contrôlée, planifiée en partie pour améliorer l'habitat des poissons indigènes, a causé une augmentation de 11 fois des taux de survie des premiers stades (de la fécondation à ~1 mois après l'émergence) des cohortes hebdomadaires de truites fécondées après la crue. Les effets d'un accroissement des fluctuations de débit durant l'incubation, calculées pour réduire l'abondance des truites, ne sont pas évidents. La mortalité à l'âge 0 entre août et septembre est deux fois plus élevée les années durant lesquelles il y a une réduction de 50 % du débit minimum par comparaison aux années à débit stable. Durant quatre des cinq années de l'étude, il existe un fort appui pour les modèles qui simulent un déplacement ontogénique vers les habitats plus profonds. L'intégration de données détaillées de terrain dans un modèle de stock synthèse pour décrire la dynamique des premiers stades de vie est une méthode précieuse qui peut être utilisée dans une gamme étendue de systèmes.

[Traduit par la Rédaction]

Introduction

Flow regulation is a widespread anthropogenic disturbance in stream environments that potentially influences both abiotic conditions in egg, larval, and juvenile habitats, as well as the intensity of biotic interactions such as competition and predation (Heggenes and Dokk 2001; Shea and Peterson 2007). Flow-related changes in growth, habitat use, and mortality of early life stages can affect recruitment of juveniles to the adult population, which in the long term potentially regulates trends in adult abundance (Elliott 1994; Lobón-Cerviá 2005). In many adaptive management settings, the evaluation of flow regimes is based solely on trends in abundance of adult populations, and inferences from flow experiments can be improved by also measuring the response of early life stages. Unfortunately, in large rivers, it can be very difficult to evaluate changes in population dynamics for early life stages because they experience high mortality rates, undergo major shifts in habitat use, and are difficult to sample, which limits application of empirical methods, such as open-

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population mark–recapture models. New approaches are needed in these systems to quantify key aspects of early life history dynamics and relate them to changes in flow.

Over the last two decades there have been considerable advances in the development of stock synthesis models (Methot 1990) that integrate multiple sources of data (e.g., catch rates, proportion of fish by age) into a single framework to jointly estimate parameters describing recruitment, growth, mortality, and abundance (e.g., Fournier et al. 1998; Eveson et al. 2004; Deriso et al. 2007). Stock synthesis models are typically applied to annual data for commercially important fish populations to provide advice for fisheries management. In this paper, we use a stock synthesis model to assess the response of early life stages of rainbow trout (*Oncorhynchus mykiss*) in the Colorado River to changes in the flow regime from Glen Canyon Dam.

Experimental flows from Glen Canyon Dam, intended to increase abundance of the endangered humpback chub (*Gila cypha*), include implementation of controlled floods and reductions in hourly fluctuations in flow to improve the quality of nearshore juvenile rearing habitat (US Fish and Wildlife Service 2008). As well, because of concerns about negative effects of rainbow trout on juvenile chub (Gloss and Coggins 2005; Yard et al. 2011), flow fluctuations were increased during winter to dewater trout redds and reduce incubation success. Inferences from studies that evaluated effects of all these experimental flows on rainbow trout were based on simple analyses (Korman et al. 2011*a*, 2011*b*) that were limited by restrictive assumptions and inability to make full use of available data. A stock synthesis model should provide more accurate and precise estimates of key population parameters and a better evaluation of flow effects.

The stock synthesis model presented in this paper estimates spawn timing and magnitude, mortality, growth, ontogenetic habitat shifts, and abundance of weekly cohorts of age-0 rainbow trout in low-angle (shallow) and high-angle (deep) habitats by fitting to redd count, length-at-age, length–frequency, and abundance data. The model provides a unified approach for evaluating alternate hypotheses concerning the effects of flow regime on early life history dynamics. We use it to evaluate effects of (*i*) nonnative fish suppression flows (redd dewatering) on early survival rates; (*ii*) a controlled flood on early survival rates (fertilization to ~1 month from emergence); and (*iii*) changes in the extent of hourly flow fluctuations during late summer and fall on age-0 survival. We compare the evaluation of hypotheses based on the stock synthesis model with those based on simpler assessments to highlight advantages and limitations of both approaches.

Materials and methods

Study area, flow regimes, and flow-related hypotheses

The Lees Ferry reach of the Colorado River, Arizona, USA, begins at Glen Canyon Dam and extends 26 km downstream to the confluence with the Paria River (see figure 1 of Korman et al. 2011*a*). The fish fauna in the Lees Ferry reach is almost exclusively nonnative rainbow trout (McKinney et al. 2001). The hydrograph is controlled by releases from Glen Canyon Dam and exhibits considerable hourly variation in flow under normal operations (the modified low fluctuating flow regime or MLFF). Nonnative fish-suppression flows (NFSF), implemented January through March 2003–2005, were intended to decrease abundance of rainbow trout by increasing hourly fluctuations to dewater redds (Korman et al. 2011*b*). Experimental flows designed to improve juvenile humpback chub habitat included a controlled flood in spring 2008 and implementation of fall steady flows (FSF) in 2008 through 2009, which eliminated the sudden reduction in the minimum flow on 1 September and stabilized flows during September and October (see figure 2 from Korman et al. 2011*a*).

Impacts of hydropeaking on juvenile fish may vary by habitat type (Bain et al. 1988; Freeman et al. 2001; Shea and Peterson 2007). In the Lees Ferry reach, hydropeaking results in a diel lateral migration of immediate shoreline areas used by juvenile fish (Korman and Campana 2009). The extent of this lateral migration will be greater in lower-angle shorelines, such as cobble bars, and less in higher-angle shorelines, such as talus slopes. The magnitude of age-0 survival responses to changes in flow variability may therefore depend on the timing of changes in flow variability relative to ontogenetic shifts in use of low- and high-angle shorelines. Describing patterns of habitat use by age-0 trout should therefore be helpful in interpreting potential flow-related trends in mortality.

Our specific expectations for experimental flow impacts on early life stages of rainbow trout were the following: (*i*) early survival rates for weekly cohorts spawned under the more variable NFSF regime will be lower than those fertilized under MLFF; (*ii*) scour and fill from the controlled flood in 2008 will reduce early survival rates for fish spawned before the flood; (*iii*) age-0 mortality will be lower between August and September under the FSF regime because of elimination of the abrupt change in minimum flow over this period; (*iv*) age-0 mortality will be lower in September and October under the FSF regime owing to steadier flows; (*v*) age-0 mortality rates for fish of similar size will be greater in low-angle shorelines than high-angle ones because the former are potentially more sensitive to hourly flow variation; and (*vi*) based on the widespread occurrence of ontogenetic shifts for juvenile salmonids towards deeper habitat as they grow, the proportion of age-0 trout moving from low- to high-angle shorelines should increase with fish size.

Field data used to parameterize the model

Data used to parameterize the model were collected in the Lees Ferry reach for 5 years between 2004 and 2009 (no data collected in 2005). The timing and magnitude of egg deposition was based on seven to eleven visual redd surveys over the entire reach each year (Korman et al. 2011*b*). Seasonal and habitat-specific trends in age-0 abundance were based on catch rates from 40 randomly selected shoreline sites, sampled on a near-monthly interval between May and November (Korman et al. 2011*a*). Juvenile sampling was conducted using backpack and boat electrofishing in low-angle (cobble bars, sand bars, and debris fans) and high-angle (talus) shoreline types, respectively. On each survey, a subsample of trout was collected for later analysis of otolith microstructure to develop length-at-daily-age relationships (Korman et al. 2011*a*). Depletion and mark–recapture experiments were conducted in 2006 and 2007 to estimate habitat-

and gear-specific relationships between capture probability and fish size (Korman et al. 2009).

Stock synthesis model overview

The stock synthesis model simulates early life history dynamics of rainbow trout and is composed of process, observation, and likelihood components. The process component predicts the recruitment of emerging fish to the age-0 population and the size and abundance of age-0 fish over summer and fall in low- and high-angle shorelines. The observation component predicts the data in the redd and age-0 survey programs, which includes the number of redds by sampling trip, catch rates of age-0 fish by length class by trip, and length-at-age. The likelihood component uses an objective function to compare the predictions with the observations. Nonlinear estimation is used to fit the parameters in the process and observation components of the model by minimizing the value of the objective function.

The model makes weekly predictions of over a 1-year period beginning 1 December. The calculations begin by predicting the number of redds in the Lees Ferry reach each week, which in turn are used to determine the number of fry from each weekly spawning cohort that emerge from the gravel. Recruitment, which we define as the total number of emergent fish per week, depends on the magnitude of egg deposition and survival from fertilization to emergence. Emergent fry are distributed to low- and high-angle habitat types. The model then predicts the number of fish in each cohort that are alive each model week in each habitat type and their size-at-age. Mortality rates of age-0 fish vary with fork length and can also vary by habitat type and over time. Size-at-age is predicted from a von Bertalanffy growth model. Each week a proportion of age-0 fish in low-angle habitat can move to high-angle habitat, and that proportion can increase with fish size. The number of fish alive at each age, time step, and habitat type is translated into predicted length frequencies based on the estimate length-at-age relationship and size-dependent vulnerability to sampling.

The model was applied to 5 of the 6 years of available field data (see table 2 from Korman et al. 2011*a*), and calculations were done separately for each year. We did not apply the model to data from 2010 because of the limited number of age-0 surveys and lack of age information. In the description that follows, model variables identified by Greek letters denote parameters that are estimated. Upper case Arabic letters denote state variables (if located to the left side of equations) or constants. Lower case Arabic letters denote indices (refer to List of symbols at end of text).

Stock synthesis model process component

The number of redds created each model week is simulated using a beta distribution (Hilborn et al. 1999)

$$(1) \qquad R_t = \chi \frac{t}{T}^{(\alpha-1)} \left(1 - \frac{t}{T}\right)^{(\beta-1)}$$

where R_t is the number of redds created in week t (with a maximum week T), χ is the total number of redds created over the entire spawning season, and α and β are parameters of the beta distribution that determine the proportion of the total redds created per week (see List of symbols). We use a convenient reparameterization of the beta distribution where the week of peak spawning (γ, the mode of the beta distribution) and the relative precision in spawn timing (α) are estimated, and β is computed as $\beta = \frac{\alpha-1}{\gamma} + 2 - \alpha$.

The number of fish that successfully emerge and recruit to the age-0 population each week (G_t) is predicted from

$$(2) \qquad G_t = \sum_t R_{t-W_t} \phi e^{-\eta_{t-W_t}}$$

where W_t is the number of weeks between spawning and emergence for each weekly cohort (the incubation period), ϕ is the maximum number of fish that can emerge per redd, and η_t is the temporal deviation in the instantaneous mortality rate over the incubation period for each weekly spawning cohort. W is a weekly constant that decreases with increases in accumulated thermal units, which were calculated based on measured intergravel water temperatures (Jensen et al. 1992; Korman et al. 2011*b*). Fish emerging on any given week can originate from more than one weekly spawning cohort because W can vary over time. ϕ represents the product of the number of eggs deposited per redd, fertilization and maximum survival rates, and a factor that accounts for any bias in the estimate of the total redds. η can either be fixed at zero to simulate the null hypothesis that there is no temporal variation in incubation success or estimated for specific blocks of weeks to evaluate the effects of seasonal changes in the flow regime from Glen Canyon Dam.

The $\phi e^{-\eta}$ term in eq. 2 represents the realized number of emergent fry per redd (per weekly cohort), which we refer to as incubation success. As we do not measure abundance at emergence, this term actually quantifies survival between fertilization and when small fry are first captured by electrofishing at 20–25 mm, about a month after emergence. We assume that differences in incubation success across years are largely caused by annual differences in mortality and that the number of eggs deposited per redd and other factors contributing to ϕ (e.g., extent of underestimation in the total number of redds) are relatively constant.

The number of age-0 trout (N) that are 1 week old ($a = 1$) in low-angle (L) and high-angle (H) habitats each model week is predicted from

$$(3) \qquad \begin{aligned} N_{L,a,t} &= G_t \delta \\ N_{H,a,t} &= G_t (1 - \delta) \end{aligned}$$

where δ is the proportion of recruits that migrate to low-angle habitat after emergence. The numbers alive in each habitat type for subsequent ages ($a = 2 \ldots A$) are predicted from

$$(4) \qquad \begin{aligned} N_{L,a,t} &= N_{L,a-1,t-1}(1 - M_a) e^{-\mu_{L,a,t}} \\ N_{H,a,t} &= (N_{H,a-1,t-1} + N_{L,a-1,t-1} M_a) e^{-\mu_{H,a,t}} \end{aligned}$$

where M_a is the proportion of fish at age a that make an ontogenetic habitat shift from low- to high-angle habitat each week, and μ is the weekly instantaneous mortality rate. Mortality can vary by habitat type, over time, and by age based on

$$(5) \qquad \begin{aligned} \mu_{h,t} &= \mu_h e^{\tau_{h,i}} \\ \mu_{h,a,t} &= \mu_{h,t} \left(\frac{l_a}{L_r}\right)^C \end{aligned}$$

where μ_h is the base mortality rate for habitat type h (low- or high-angle), i is an index for the block of weeks between each sampling period, $\varepsilon_{h,i}$ is the temporal mortality deviation for each block of weeks (note $\sum_i \varepsilon_{h,i} = 0$), l_a is the fork length for fish of age a, L_r is the reference fork length where the mortality rate is $\mu_{h,t}$, and C is the allometric exponent of the mortality – fork length relationship, which was fixed at –1 (Lorenzen 2000).

Ontogenetic movement is assumed to be unidirectional from low- to high-angle habitats and can depend on size based on the following logistic function

$$(6)\qquad M_a = \frac{\rho_0}{1 + e^{-\left(\frac{l_a - \rho_\mu}{\rho_\sigma}\right)}}$$

where ρ_0 is the maximum proportion moving per week, ρ_μ is the fork length where the proportion moving is 50% of the maximum rate, and ρ_σ is the standard deviation of the fork length – movement relationship.

The prediction of mean length-at-age is based on a reparameterization of the von Bertalanffy growth model (Schnute and Fournier 1980)

$$(7)\qquad l_a = \lambda_1 + (\lambda_A - \lambda_1)\frac{1 - e^{-\kappa(a-1)}}{1 - e^{-\kappa(A-1)}}$$

where λ_1 and λ_A are fork lengths at emergence ($a = 1$) and at 52 weeks from emergence ($a = A$), respectively, and κ is the von Bertalanffy metabolic parameter. The relationship between length and age for age-0 rainbow trout in the Lees Ferry reach determined from otoliths was very linear (see figure 7 in Korman et al. 2011*a*) but was only based on fish that were generally less than 6 months old. The stock synthesis model must predict length for fish that could be up to 10 months old, and there is information about length-at-age in the length–frequency data given knowledge about emergence timing from the redd surveys. The von Bertalanffy model has the flexibility to accommodate reduced growth for larger fish if that trend is supported by this ancillary data.

Stock synthesis model observation component

The predicted number of redds present on each model week ($\widehat{r}_t$) is calculated as the difference between the cumulative number of redds created (eq. 1) and the cumulative number that have faded (F_t)

$$(8)\qquad \widehat{r}_t = \sum_t R_t - \sum_t F_t$$

A redd is designated as faded when it exceeds its survey life (S in weeks) and is therefore no longer visible to an observer (i.e., $F_t = R_{t-S}$). S is a constant that was estimated based on a geographic information system (GIS) analysis of changes in redd locations over time (Korman 2009).

Assuming variation in length-at-age is normally distributed, the total probability of a fish being in a length class centered on x at age a is calculated as

$$(9)\qquad P_{j,a} = \frac{1}{\sigma_a\sqrt{2\pi}} \int_{x-\frac{w}{2}}^{x+\frac{w}{2}} e^{-\frac{(x-l_a)^2}{2\sigma_a^2}}\,dx$$

where w is the width of each length interval (5 mm), j is the index for the length interval $x - w/2$ to $x + w/2$, and σ_a is the standard deviation in length-at-age. Error in length-at-age is assumed to be normally distributed with estimated mean l_a, with σ_a computed as $l_a v_l$, where v_l is the estimated coefficient of variation in length-at-age.

The vulnerability of age-0 fish to capture by electrofishing is assumed to vary by habitat type and with fork length according to the logistic function

$$(10)\qquad V_{h,a} = \frac{\pi_h}{1 + e^{-\left(\frac{l_a - \psi_h}{\tau_h}\right)}}$$

where $V_{h,a}$ is the detection probability in habitat type h for fish of age a within sampling sites, π_h is the proportion of the population captured within sampling sites that are large enough to be fully vulnerable to capture, and ψ_h and τ_h are the length at which vulnerability to sampling is 50% of the maximum and the standard deviation of the fork length – vulnerability logistic function, respectively.

The predicted number of fish caught in habitat type h in sample week t within length interval j ($\widehat{C}_{h,t,j}$) is computed from

$$(11)\qquad \widehat{C}_{h,t,j} = E_{h,t}\sum_a V_{h,a}P_{j,a}N_{h,a,t}$$

where $E_{h,t}$ is the sampling effort by habitat type and week, expressed as the proportion of shoreline length in the Lees Ferry reach that is electrofished on each sampling trip for each habitat type. The product of habitat-specific effort and vulnerability represents the proportion of fish caught within the total shoreline length of the reach for each habitat type.

Stock synthesis model likelihood component

We use a maximum likelihood approach to jointly estimate year-specific parameters that predict redd counts, length-at-age, and catch data by habitat type, sampling trip, and size class. An independent likelihood term is defined for each type of data. Error in redd count, length-at-age, and catch data are assumed to follow Poisson, normal, and Poisson distributions, respectively. The negative log likelihood for the Poisson model for redd counts (NLL_r), omitting the scaling constants that do not affect the estimation, is

$$(12)\qquad \mathrm{NLL}_r = \sum_t \widehat{r}_t - \widetilde{r}_t \log(\widehat{r}_t)$$

where $\widetilde{r}_t$ and $\widehat{r}_t$ are the observed and predicted number of redds, respectively, on sample week t. The negative log likelihood for the length-at-age data (NLL_{la}) omitting constants is

$$(13)\qquad \mathrm{NLL}_{la} = \sum_k \log(\sigma_{l,k}) + \frac{(\widetilde{l}_k - \widehat{l}_k)^2}{2\sigma_{l,k}^2}$$

where $\widetilde{l}_k$ and $\widehat{l}_k$ are the observed and predicted length, respectively, for fish of known age, k is the index for each length-at-age observation, and $\sigma_{l,k}$ is the standard deviation for each observation computed as $\sigma_{l,k} = \widehat{l}_k v_l$. The negative log likelihood for catch data (NLL_C) omitting constants is

$$(14)\qquad \mathrm{NLL}_{c,h} = \sum_t \sum_j \widehat{C}_{h,t,j} - \widetilde{C}_{h,t,j} \log(\widehat{C}_{h,t,j})$$

where $\widetilde{C}_{h,t,j}$ is the observed catch in habitat type h, sample week t, and size class j.

The model was programmed using AD Model Builder (ADMB, Otter Research 2004). Model source code, executable, estimation control and data files, and R graphic scripts are available online in the supplementary data[2] . Maximum likelihood estimates for parameter values were estimated by minimizing the total negative log likelihood (NLL_T)

$$(15) \qquad NLL_T = NLL_e + NLL_{\hat{a}} + NLL_{\tau,L} + NLL_{\tau,H}$$

All parameters were estimated in an untransformed state except for ρ_0, which was logit-transformed to ensure values ranged from 0 to 1. We did not estimate parameters for the size–vulnerability relationship (eq. 10) within the stock synthesis model and instead fixed them at their maximum likelihood estimates determined from 2-day mark–recapture experiments (Korman et al. 2009).

To ensure that a global minimum was found, a minimum of 10 different random initial conditions were used to estimate parameters. Initial values used in the ADMB search were randomly drawn from bias-corrected, log-normal distributions centered around base initial values (Table 1). Asymptotic estimates of the standard error of parameter estimates and the covariance among parameters (Pearson's correlation coefficient) at their maximum likelihood values were computed from the Hessian matrix within ADMB.

Evaluation of alternate hypotheses of early life history dynamics

A series of nested models were used to evaluate alternate hypotheses concerning incubation success (recruitment), age-0 mortality, and ontogenetic habitat shifts. Two models were used to evaluate the effect of nonnative fish-suppression flows and the controlled flood on incubation success. In 2004 and 2008, flows intended to dewater redds, and a controlled flood, ended on 31 March and 9 March, respectively. We evaluate whether weekly cohorts fertilized prior to 21 March (model week 16, the approximate midpoint between these events), which were subject to dewatering and scour, had reduced incubation success relative to cohorts fertilized after this date. The null recruitment model (R1) assumes that the seasonal variation in the numbers of age-0 trout emerging from the gravel each week depends on spawn timing (eq. 1) and time required for incubation (W) only and also assumes that incubation success is identical for all weekly cohorts before and after 21 March (Table 2). The seasonal recruitment model (R2) estimates a single incubation mortality rate that is applied to all cohorts spawned before 21 March ($\eta_1 = \eta_{2,...} = \eta_{16}$) and assumes no additional mortality for cohorts spawned after this date. A comparison of differences in η_{1-16} and η_{17-52} (fixed at zero) in 2004 and 2008, and with other years, can be used to determine if these flow events had substantive effects on incubation success.

We examine four nested models to evaluate the effects of the FSF regime on age-0 mortality and differential effects of mortality between habitat types. The null mortality model assumes that mortality rates in low- and high-angle habitat are equal and constant through time (M1; Table 2). The habitat-dependent model estimates habitat-specific mortality rates that do not change over time (M2). The next complex mortality model allows mortality rates to vary over time but not between habitat types (M3). The most complex model allows mortality to vary over habitat type and time (M4). Three alternate models simulating an ontogenetic habitat shift from low- to high-angle shorelines were examined: a null model that assumes no movement (O1); a size-independent model where the proportion moving each week is constant (O2); and a size-dependent model where the proportion moving each week increases with fork length (O3).

We examined all 24 combinations of recruitment, mortality, and ontogenetic shift models and identify model combinations by concatenating codes. For example, R2-M3-O1 refers to a model based on recruitment model R2, mortality model M3, and ontogenetic movement model O1. All 24 models were fit to the data from each year and compared (within years) using the Akaike's information criteria (AIC). When comparing a range of candidate models, the model with the lowest AIC value loses the least amount of information, that is, achieves the best balance between bias and precision, and will therefore have the best predictive performance when applied to replicate data sets. Models with similar AIC values relative to the best model (ΔAIC = 0–2) are considered to have strong support, while those with larger AIC values are considered to have moderate (ΔAIC = 4–7) or essentially no ($\Delta AIC > 10$) support (Burnham and Anderson 2002).

Simulation exercise to evaluate the reliability of stock synthesis parameter estimates and model selection

A simulation model was used to generate synthetic data based on known parameters, which in turn was used to evaluate the accuracy of parameter estimates and the ability of the AIC method to identify the correct data-generating model structure. Error in generated data was simulated using the rejection method (Press et al. 1992) based on the same error models used in the estimation. Length-at-age samples were generated by simulating the stratified-sampling approach used in the field program, where a fixed number of samples were taken from each unique habitat type, sampling trip, and 10 mm length interval combination (Korman et al. 2011*a*). The maximum length of fish sampled for ageing was set at 90 mm to approximate the maximum size of fish that were aged in the field study. Two levels of redd sampling and age-0 sampling were simulated: a high-resolution simulation was based on 11 redd surveys and eight age-0 surveys per year, similar to sample timing and effort in 2004, 2008, and 2009; and a lower-resolution simulation based on seven redd surveys and five age-0 surveys per year, corresponding to sample timing and effort in 2006 and 2007.

Bias in maximum likelihood estimates was evaluated using Monte Carlo simulations, where we compared average parameter estimates across 100 trials with the true values used to simulate the data (% bias = 100 × (estimate – true)/true). Simulations were conducted based on recruitment model R1 for all six combinations of mortality models M1 and M2 and ontogenetic movement models O1, O2, and O3 (Table 2). We applied all six estimation models to data generated from each

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[2] Supplementary data for this article are available on the journal Web site (http://nrcresearchpress.com/cjfas).

Table 1. Summary of initial values and lower and upper bounds for parameters of the estimation model and parameters used to generate data for the simulation analysis.

	Estimation		Simulation		
Parameter	Initial values	Lower and upper bounds	All cases		
χ	200	10–5000	2000		
γ	15	1–40	15		
α	10	1–500	10		
η_t	0	0–5	0		
ϕ	1000	$100–1 \times 10^6$	1000		
δ	0.56	0.001–1	0.56		
κ	0.005	0.001–5	0.015		
λ_1	20	1–50	20		
λ_A	150	100–200	135		
$\varepsilon_{h,t}$	0	–1.5–1.5	0		
ν_l	0.1	0.01–0.3	0.1		
π_h	$L = 0.34$, $H = 0.31$	Fixed	$L = 0.34$, $H = 0.31$		
ψ_h	$L = 26.61$, $H = 39.89$	Fixed	$L = 26.61$, $H = 39.89$		
τ_h	$L = 2.60$, $H = 4.57$	Fixed	$L = 2.60$, $H = 4.57$		
			M1	**M2**	
μ_L	0.1	0.001–2	0.1	0.15	
μ_H	0.1	0.001–2	0.1	0.05	
			O1	**O2**	**O3**
ρ_0	0.27	0–1	0	0.15	0.15
ρ_μ	50	1–150	10	10	50
ρ_σ	5	$0.1–1 \times 10^6$	0.1	0.5	2

Note: *L* and *H* denote low- and high-angle habitat, respectively. Parameters where the lower and upper bounds are denoted as "Fixed" indicate that the parameters are held constant at the initial values. See Table 2 and List of symbols for definition of parameters and simulation cases.

Table 2. Parameterization for alternate models of incubation success (recruitment, R), age-0 mortality (M), and ontogenetic habitat shifts (O).

Model type	Model description	Model code	Estimated parameters	Fixed parameters
Recruitment	Null	R1	—	$\eta_t = 0$
	Reduced incubation success up to week 16	R2	$\eta_1 = \eta_{2\ldots} = \eta_{16}$	$\eta_{17\text{–}52} = 0$
Mortality	Null (single value)	M1	μ_L	$\mu_H = \mu_L$, $\varepsilon_{h,t} = 0$
	Mortality varies between habitats	M2	μ_L, μ_H	$\varepsilon_{h,t} = 0$
	Mortality varies over time	M3	μ_L, $\varepsilon_{L,t}$	$\mu_H = \mu_L$, $\varepsilon_{H,t} = \varepsilon_{L,t}$
	Mortality varies with time and habitat	M4	μ_L, μ_H, $\varepsilon_{h,t}$	—
Ontogenetic habitat shift	No ontogenetic shift	O1	—	$\rho_0 = 0$, $\rho_\mu = 10$, $\rho_\sigma = 0.1$
	Size-independent shift	O2	ρ_0	$\rho_\mu = 10$, $\rho_\sigma = 0.1$
	Size-dependent shift	O3	ρ_0, ρ_μ, ρ_σ	—

Note: See List of symbols for definition of parameters.

simulation model to compare bias when both correct and incorrect model structures were applied to the synthetic data. We also evaluated the ability of the AIC model selection procedure to identify the correct data-generating model. AIC statistics were computed for each estimation model on each trial. We then compared AIC scores across estimation models within trials and computed the percentage of trials where the correct data-generating model was identified. In cases where the correct model was identified, we computed the average difference between the lowest AIC score and the next lowest AIC score to determine the typical degree of support for alternate models.

Results

Evaluation of bias and model selection via simulation

There was little bias in estimated parameters when the same model structures were used for simulation and estimation (Table 3). For brevity, we show results for the low-resolution sampling case only, which provides a worst-case scenario. Bias in most model parameters was generally less than 5%. The von Bertalanffy metabolic coefficient (κ) had a slightly larger bias ranging from 4% to 10%, which was caused by an overrepresentation of faster-growing fish in the simulated sample because of size-dependent differences in

Table 3. Bias (%) in model parameters based on recruitment model R1 and alternate mortality (M) and ontogenetic habitat shift (O) models for the low-resolution sampling regime and the same simulation and estimation model types.

	Bias (%)					
Parameter	M1-O1	M2-O1	M1-O2	M2-O2	M1-O3	M2-O3
χ	1.2	2.2	2.4	0.4	0.4	0.4
γ	2.0	3.4	4.0	0.5	0.5	0.5
α	2.6	1.1	0.6	2.5	3.0	2.9
ϕ	–4.3	–4.2	–5.4	–4.8	–3.5	–2.9
δ	0.1	–0.1	–0.5	–1.6	0.3	0.4
κ	10.5	5.6	6.4	3.6	9.4	7.8
λ_I	0.6	1.0	1.4	1.1	0.2	0.1
λ_A	–1.9	–1.3	–1.4	–0.5	–1.3	–1.0
η_I	6.4	4.4	4.0	3.2	4.9	3.8
ρ_0	—	—	–0.1	–1.8	–1.7	–5.7
ρ_b	—	—	—	—	0.6	3.8
ρ_v	—	—	—	—	–20.8	3.4
μ_L	–2.3	–1.3	–2.6	–4.4	–1.2	–0.6
μ_H	—	–5.0	—	–1.5	—	–2.5
Mv_22.5	0.00	0.00	0.00	0.01	0.00	0.00
Mv_42.5	0.00	0.00	0.00	0.01	0.00	0.00
Mv_62.5	0.00	0.00	0.00	0.01	0.00	0.00
Mv_82.5	0.00	0.00	0.00	0.01	0.00	0.01

Note: The last four rows show the difference between the estimated and true simulated proportion moving from low- to high-angle habitat types per week for fish with fork lengths of 22.5, 42.5, 62.5, and 82.5 mm. See List of symbols and Table 2 for definition of model parameters and structures, respectively.

vulnerability (as shown in Taylor et al. 2005). Ontogenetic movement parameters had little bias with the exception of ρ_v, which was underestimated by approximately 20%. Although this bias was substantial because of confounding among movement parameters (see Supplemental Table S1.1[2]), there were negligible differences in realized movement rates across a wide range of fish sizes (e.g., Mv_22.5 to Mv_82.5 values in Table 3). There was little bias in cases where the structure of the estimation model was more complex than that of the data-generating model (results not shown for brevity). However, substantial biases in mortality, movement, and some growth (κ) and recruitment (ϕ, δ) parameters occurred in cases where the estimated mortality or movement models were simpler than the models used to generate the data.

The AIC method reliably identified the model used to generate simulated data under a range of model structures for both sampling regimes (Table 4). The data-generating model was identified correctly at a minimum rate of 82% (M1-O2) and a maximum rate of 99% (M2-O3). In four (low-resolution sampling) or five (high-resolution sampling) of the six cases, the correct generating models were identified at a rate of 90% or higher. There was minimal loss of information (small differences in AIC) in cases where more complex estimation models were applied to data generated from relatively simple simulation models. As model complexity increased, there were larger differences in AIC scores because the reduced fit associated with applying simpler models to data generated from a more complex process outweighed the benefits of increased precision owing to the reduction in the number of parameters. There was little effect of sampling intensity (low- vs. high-resolution) on AIC model identification performance.

Evaluation of alternate models describing early life history dynamics based on data

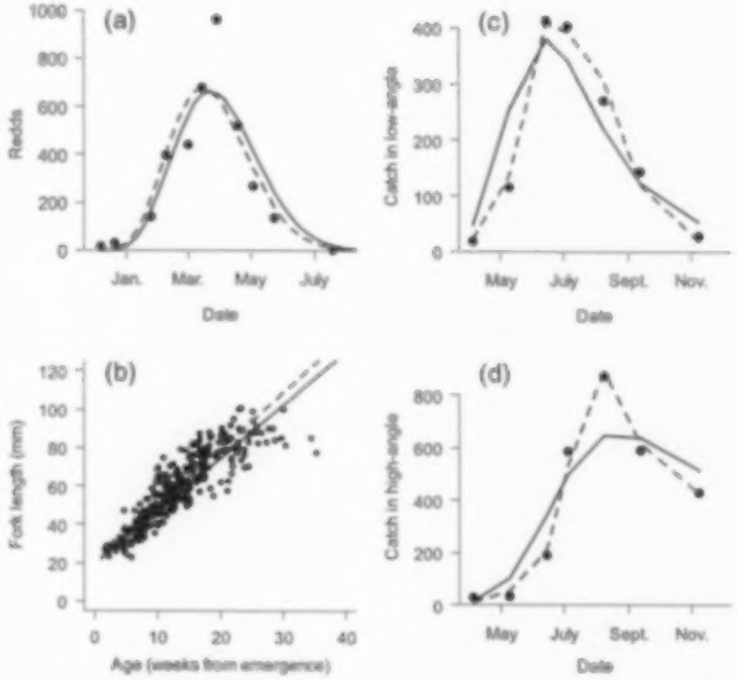
The AIC analysis indicated that the most complex of the 24 models that were evaluated (R2-M4-O3) had the best predictive power in most years. Complex models with more parameters generally fit the data much better than simpler ones, as illustrated by a comparison of fits of R1-M2-O1 and R2-M4-O3 to the 2004 data (Figs. 1 and 2). In this example, the AIC score for the more complex model with 29 parameters was 734 units lower than the score for the simpler model with 17 parameters. There was strong support for models that allowed age-0 mortality to vary between habitat types and sampling trips (M4) in all years (Fig. 3). There was strong support for models that allowed seasonal variation in incubation mortality (R2) and size-dependent ontogenetic movement from low- to high-angle shorelines (O3) in 2004, 2007, and 2008. There was less evidence for temporal variation in incubation mortality in 2006 and 2009 and less evidence for ontogenetic movement in 2006. Maximum likelihood estimates were consistent with results from the AIC analysis (Table 5). For example, estimates of incubation mortality before 21 March (η_{1-16}) were greater in years when model R2 was strongly supported (2004, 2007, and 2008). The maximum likelihood estimate of the maximum proportion of age-0 trout moving from low- to high-angle shoreline (ρ_0) was zero in 2006, the only year when there was strong support for model that did not simulate ontogenetic movement (O1).

Table 4. Assessment of the Akaike information criteria (AIC) to identify the correct data-generating model.

Simulation type		Low-resolution		High-resolution	
Mortality	Movement	% correct identification	Avg. ΔAIC	% correct identification	Avg. ΔAIC
M1	O1	93	1.59	94	1.63
M2	O1	91	1.81	95	1.84
M1	O2	82	1.49	83	1.56
M2	O2	91	2.87	96	3.65
M1	O3	89	9.42	90	5.16
M2	O3	99	22.70	98	42.25

Note: 100 data sets were generated from each of six alternate simulation models. AIC statistics were then computed by estimating parameters for all models applied to each of the 100 trials for each set of simulations. The percentage of trials where the correct data-generating model was identified, and the average difference between the lowest AIC and the next lowest AIC for these cases, are shown for both low- and high-resolution sampling regimes. See Table 2 for definition of alternate model structures.

Fig. 1. Comparison of the fit of models R1-M2-O1 (solid lines) and R2-M4-O3 (dashed lines) to data from 2004. Panels *a*–*d* show predicted (lines) and observed (solid circles) redd counts (*a*), length-at-age (*b*), and catch in low-angle (*c*) and high-angle (*d*) habitats. See Table 2 for definition of model structures.

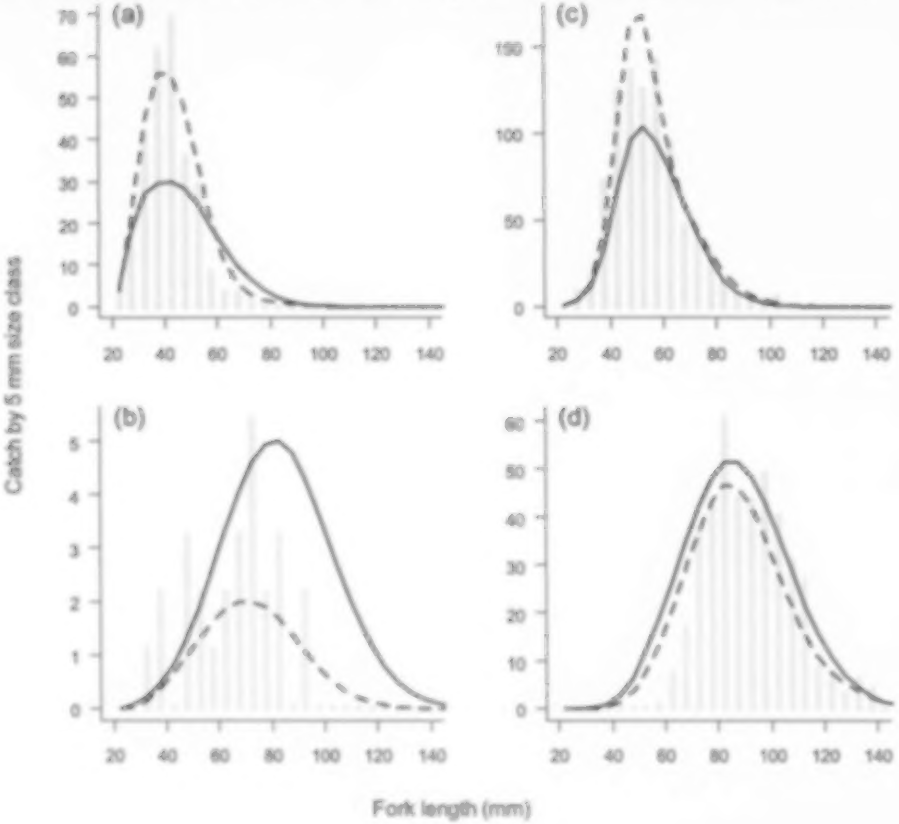


Effects of nonnative fish suppression flows and a controlled flood

The effects of nonnative fish-suppression flows on early life stages were not evident. Incubation mortality prior to 21 March was higher in 2004 when NFSF was implemented, and such a difference was not apparent in 2009 under normal operations when there were limited differences in hourly variation before and after this date (η_{1-16} in Table 5; Fig. 4). However, reduced incubation success prior to 21 March was also seen in other years under normal operations (excluding 2008 because of the confounding effect of the controlled flood).

Contrary to our predictions, the controlled flood did not reduce survival for cohorts that were still incubating in the gravel when the flood occurred, but instead increased survival for cohorts fertilized after the event. Incubation success for cohorts fertilized before 21 March in 2008 was over threefold greater than in 2007 under normal operations. In 2008, incubation success for cohorts fertilized after the flood were 11-fold higher compared with those for cohorts fertilized before it (η_{1-16} in Table 5; Fig. 4) and threefold higher relative to cohorts fertilized after 21 March in other years (2006 excluded because of the confounding effect of reduced density-dependent mortality).

Fig. 2. Comparison of the fit of models R1-M2-O1 (solid lines) and R2-M4-O3 (dashed lines) to catch-at-length data (vertical bars) from 2004. Graphs show results for low-angle habitat in August (*a*) and November (*b*) and high-angle habitat in August (*c*) and November (*d*). The fit to data from other months sampled in 2004 are not shown for brevity. See Table 2 for definition of model structures.



Effects of the fall steady flow regime

The sudden decrease in the minimum flow between August and September under normal operations (MLFF 2004–2007) resulted in age-0 mortality rates that were twofold higher compared with years when there was no change in the minimum flow (FSF 2008–2009; Fig. 5). As well, mortality rates between August and September under normal operations were over threefold higher than in adjacent months. Contrary to our expectation, fall (September–November) mortality rates were higher under steady flows (FSF 2008–2009) relative to normal operations.

Evidence for an ontogenetic habitat shift and differences in mortality rates between habitat types

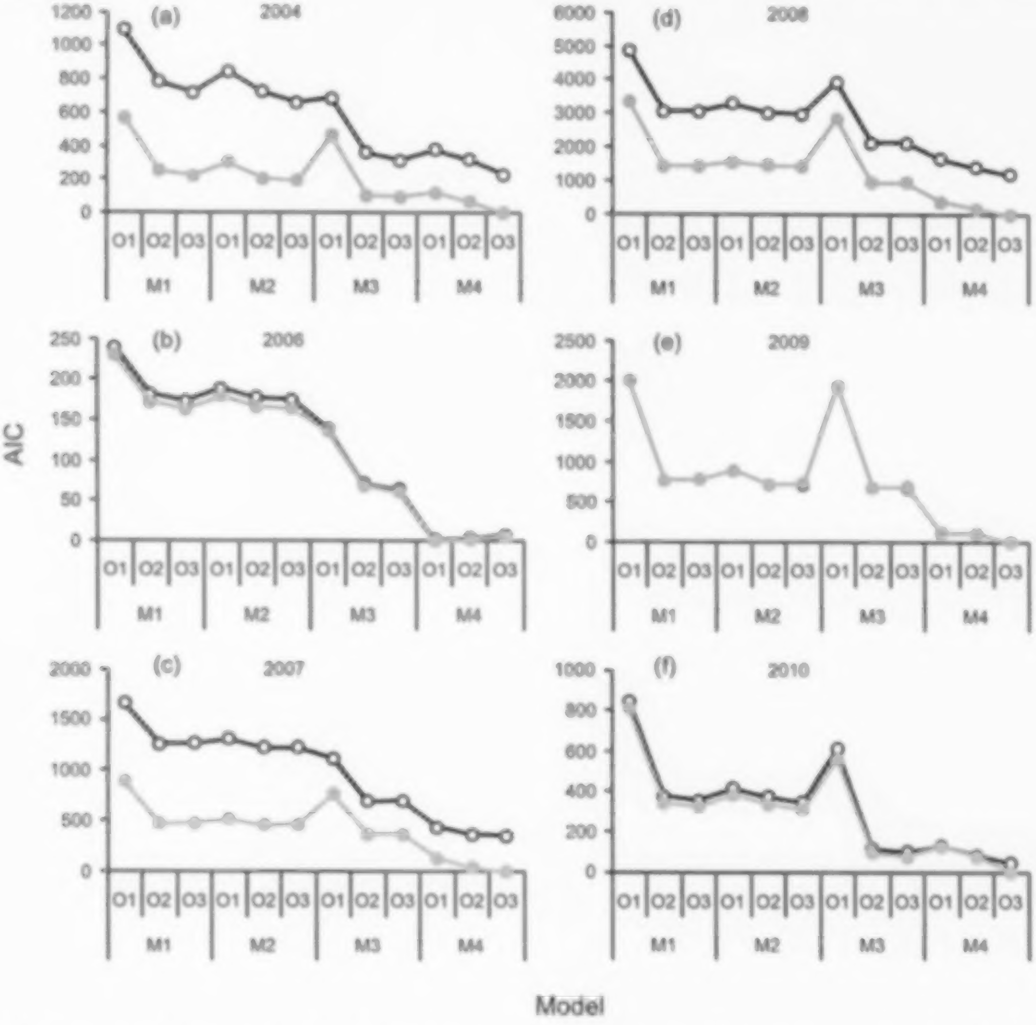
There was strong support for models that allowed size-dependent ontogenetic movement from low- to high-angle shorelines in all years except 2006 (Fig. 3), when sampling in both habitat types only began in July. Movement parameters indicated that approximately 10% of fish between 40 and 50 mm migrated from low- to high-angle shorelines each week (Table 5; ρ_b, ρ_μ). There was more evidence for differences in mortality over time (ΔAIC of M1 vs. M3, M2 vs. M4) relative to differences between habitat types (ΔAIC of M1 vs. M2, M3 vs. M4). Consistent with this result, there was considerable uncertainty in habitat-specific estimates of mortality, and in most years the confidence intervals overlapped (Fig. 6). In years when this was not the case (2006 and 2008), mortality in low-angle shorelines was 25% greater than that in high-angle shorelines.

Discussion

The stock synthesis model we developed was useful for quantitatively evaluating a range of hypotheses about the effects of flow on population dynamics for early life history stages of rainbow trout. Simulation results indicate that the model provides relatively accurate and precise estimates of parameters defining mortality, growth, and ontogenetic habitat shifts for age-0 trout based on the levels of sampling effort achieved in the field study. It also indicated that an information-theoretic approach can correctly rank alternate models describing these dynamics. Application of the model to 5 years of data indicated that incubation success and age-0 mortality rates were affected by flow and abundance.

Estimates of incubation success from the stock synthesis model are partially confounded with age-0 mortality rates for recently emerged fish. What we term "incubation success" actually reflects survival rates for early life stages between fertilization and approximately 1 month from emergence,

Fig. 3. Differences in Akaike information criteria (AIC) scores of 24 alternate models relative to the model with the lowest score for each year (ΔAIC = 0). Black lines with open circles and gray lines with filled circles denote AIC differences based on recruitment models R1 and R2, respectively. Comparisons are based on fits to data from 2004 (*a*), 2006 (*b*), 2007 (*c*), 2008 (*d*), and 2009 (*e*). See Table 2 for definition of model structures.



when age-0 trout become large enough (~20–25 mm) to recruit to the sampling gear (Korman et al. 2009). In 2006, the number of redds estimated by the spawning model was 13- to 25-fold lower than in other years, yet age-0 abundance declined by only 2.5- to 3-fold (Korman et al. 2011*b*). This potentially indicates a strong compensatory response in early survival rates at low abundance, which is consistent with the high estimate of fry per redd in 2006 compared with other years. Additional observations at low spawner abundance are critical to reduce uncertainty in the strength of this compensatory response.

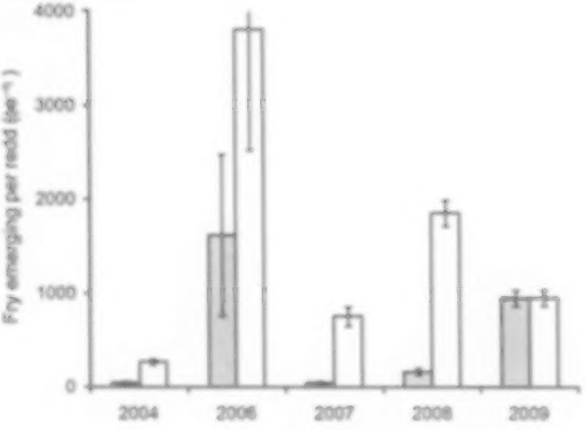
There was no evidence that nonnative fish-suppression flows, designed to dewater redds, reduced early survival rates. Early survival was lower for weekly cohorts fertilized prior to 21 March in 2004, when 50% of the redds were dewatered (Korman et al. 2011*b*) compared with later in the year when few redds were dewatered, and survival was similar for early and late cohorts in 2009 under normal operations when few redds were dewatered during either period. However, lower survival for early cohorts was also observed in 2006 and 2007 when the extent of dewatering was minimal and similar between periods. This conclusion is consistent with those from simple hatch date and stock recruit analyses of the same information (Korman et al. 2011*b*) and indicates that strong density dependence in mortality shortly after emergence may compensate for losses associated with redd dewatering. Conclusions based on the stock synthesis model are more robust because the model provides estimates of uncertainty in early survival rates for cohorts fertilized before and after the flow change. As well, the model does not require restrictive assumptions that could lead to bias in estimates of early survival rates, such as a constant age-0

Table 5. Maximum likelihood estimates for model R2-M4-O3.

Parameter	2004	2006	2007	2008	2009
χ	2273	88	1210	2032	1651
γ	13.5	16.9	13.6	16.0	17.2
α	5.6	7.7	4.8	7.3	11.2
ϕ	272	3,809	758	1,854	951
η_{1-16}	1.75	0.86	2.79	2.39	0.00
δ	0.51	0.37	0.66	0.77	0.76
κ	0.001	0.034	0.008	0.003	0.049
λ_1	22	25	25	25	26
λ_A	172	124	159	182	110
ν_1	0.15	0.12	0.10	0.11	0.15
ρ_0	0.20	0.00	0.15	0.20	0.16
ρ_a	39	79	39	48	46
ρ_w	0.10	0.13	0.10	5.66	0.12
μ_L	0.03	0.13	0.03	0.10	0.10
μ_H	0.06	0.10	0.06	0.08	0.10
No. of parameters	29	25	25	29	27

Note: See List of symbols and Table 2 for definition of model parameters and structures, respectively. The number of parameters in the model for each year (bottom row) varies with the number of temporal mortality deviates ($\varepsilon_{k,t}$), which depends on the number of sampling trips each year. Mortality deviates are not shown for brevity, but see Fig. 5 for mortality rates for some periods.

Fig. 4. Maximum likelihood estimates of the number of fry emerging per redd before (shaded bars) and after (open bars) 21 March in 2004 when fluctuations prior to this date were greater (nonnative fish-suppression flow or NFSF), under normal fluctuations (2006–2009), and in 2008 when a controlled flood occurred prior to this date. Results are based on maximum likelihood estimates for model R2-M4-O3. See List of symbols and Table 2 for definition of model variables and structures, respectively. Error bars denote 95% confidence intervals.



mortality rate across trips, which cannot be avoided in a traditional hatch date analysis.

The stock synthesis model also provided a stronger inference about the effect of the 2008 controlled flood because it quantified differences in early survival rates within and among years. The model estimated an 11-fold increase in early survival rates for cohorts fertilized after 21 March in 2008 relative to those fertilized before this date, and the AIC analysis indicated the extent of support for the recruitment model that accommodated such seasonal variation was greatest in 2008. A simpler hatch date analysis of the same data (Korman et al. 2011*b*) also indicated that early survival for cohorts fertilized after the flood was higher. However, because of the limitations of the simple analysis, the extent of the differences in survival between early and late cohorts in 2008, and between years, could not be quantified. The stock synthesis model indicated that the flood enhanced early survival rates for cohorts fertilized after the flood but did not reduce survival for earlier cohorts and that after-flood survival rates for the later cohort were exceptionally high compared with other years.

We hypothesized that steadier flow from Glen Canyon Dam would decrease mortality for age-0 trout in late summer and fall. The elimination of the sudden reduction in the minimum flow between August and September under the FSF regime did reduce mortality compared with estimates under normal operations. However, mortality was higher in the fall under stable flows compared with normal operations when flows fluctuated. These differences are consistent with those from a simpler analysis based on rates determined from the ratio of abundance estimates across sampling trips (Korman et al. 2011*a*). However, inferences from the assessment based on the stock synthesis model are stronger because (*i*) estimates of seasonal variation in mortality will not be biased by changes in recruitment of emergent fish into the age-0 population and increasing fish size over the growing season; (*ii*) mortality estimates will be more precise than those from the abundance ratio method because of the added information incorporated in the model; and (*iii*) mortality from August to September could be compared with rates from July to August, which was not possible using the abundance ratio method owing to the decrease in recruitment to the age-0 population over this period (see (*i*) above).

There was strong support for a size-dependent ontogenetic

Fig. 5. Maximum likelihood estimates of the daily instantaneous mortality rates ($\mu/7$) for age-0 trout during summer when flow and hourly fluctuations in flow are higher (July–August, open circles), the minimum flow transition period (August–September, black filled circles), and lower and steadier flows in fall (September–November, gray filled circles). Error bars denote 95% confidence intervals. Results are based on model R2-M3-O3.

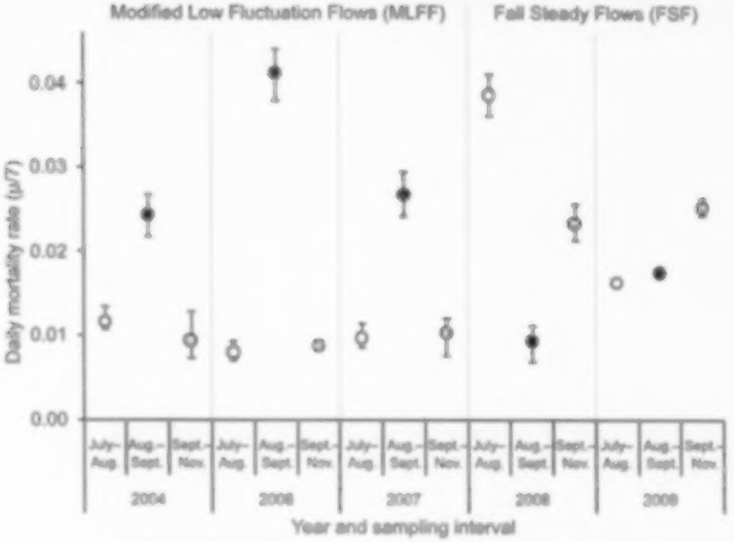
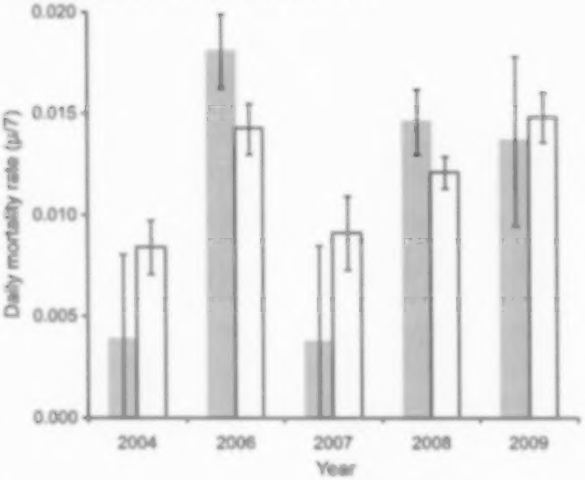


Fig. 6. Maximum likelihood estimates of the daily instantaneous mortality rate ($\mu_A/7$) in low-angle (shaded bars) and high-angle (open bars) habitat types. Results are based on model R2-M4-O3. Error bars denote 95% confidence intervals.



habitat shift of age-0 trout from low- to high-angle shorelines in most years and very limited support that age-0 mortality was more sensitive to flow variation in low-angle shorelines. Habitat-specific mortality rates could not be computed using the abundance ratio method (Korman et al. 2011*a*) because it could not account for ontogenetic movement. However, habitat-specific mortality rates estimated by the stock synthesis model were imprecise because of confounding between ontogenetic movement and mortality parameters (see Supplemental Table S1.1[2]) even with some relatively restrictive structural assumptions (i.e., equal growth among habitat types, equal effect of size on mortality rate). Direct estimates of mortality and movement based on tagging, or mesocosm experiments, where effects of density and movement can be controlled or removed, are required to quantify differences in mortality among habitat types.

Quantifying temporal changes in mortality rates within a year (e.g., across months) to make inferences about flow effects is a unique and important element of our analysis. The within-year approach maximizes the strength of inference that can be derived from relatively short-term flow experiments where the number of annual replicates is limited, a common situation in many adaptive management settings. The stock synthesis model provides a much sharper interpretation of within-year patterns than simpler approaches (e.g., Korman et al. 2011*a*). However, among-year comparisons are still needed to determine whether within-year patterns are consistent for a given flow regime and to account for differences in mortality owing to density dependence. Life-stage-specific estimates of mortality provided by the model each year include effects of both flow and density dependence. These effects were partially separated in our analysis by comparing mortality rates across years with contrasting abundance levels and flow regimes (within constraints imposed by limited sample size). Alternatively, we could have included additional density-dependent mortality terms directly in the model by simultaneously estimating parameters for all years. This joint-estimation approach would be more informative than the year-independent approach used here, but requires more years of data coupled with sufficient contrast to allow statistical separation of flow and density effects.

There are some limitations and assumptions in the stock synthesis model that warrant caution when interpreting results. Simplifying assumptions in the observation component likely underestimate the uncertainty of parameter values. For example, the catch data are pooled across sites sampled on each trip, and the likelihood for catch-at-length assumes that all fish are independent samples from the larger population. Ultimately, such assumptions may lead to confidence intervals that are too narrow and differences in AIC scores among models that are too large. This limitation would not affect the ordering of alternate models, but would result in an underestimate in the degree of support for simpler ones. These shortcomings could be addressed by including overdispersion in the catch-at-length likelihood component or by modeling catch-at-length at the site level using a hierarchical approach.

Inferences about effects of flow regulation and other anthropogenic factors on adult fish populations will be stronger if the impacts on early life history dynamics are quantified. The sampling strategy and stock synthesis modeling approach developed here is an effective method to quantify these dynamics and could be applied to other species and river systems. The model improves the interpretation of data within years, but strong inference about flow and density-dependent effects ultimately requires a sound experimental design with adequate, multiyear replication combined with process-oriented studies to help establish cause-and-effect relationships.

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List of symbols

Indices and maximum index values

t, T model week index (t = 1–52) and terminal week (T = 52)
a, A age index for fish cohorts, in weeks (1–52) and terminal age (A = 52)
i index for blocks of weeks between each age-0 sampling trip
j length interval index (1–31, representing 5 mm size classes from 20 to 175 mm)
k length-at-age sample index
h low-angle ($h = L$) or high-angle ($h = H$) habitat type

Constants

S redd survey life (4 weeks)
W_t number of weeks between fertilization and emergence (8–10 weeks)
C allometric exponent of the mortality – fork length relationship (C = –1, unitless)
L_r reference fork length for allometric mortality – fork length relationship (50 mm)
$E_{h,i}$ effort (proportion of shoreline length sampled by type and trip)

Estimated parameters for process model

χ total redds excavated per year
γ week of peak spawning
ω relative precision in spawn timing (weeks)
η_t temporal deviation in the instantaneous incubation mortality rate
ϕ maximum number of fry that emerge per redd
δ proportion of fry that migrate to low-angle habitat after emergence
μ_h base weekly instantaneous mortality rate by habitat type
ρ_0 maximum proportion moving from low- to high-angle habitat per week
ρ_μ fork length (mm) at which movement rate is reduced to 50% of the maximum (ρ_0)
ρ_σ standard deviation (inverse of slope) of movement – fork length relationship (mm)
κ von Bertalanffy metabolic coefficient (unitless)
λ_1 fork length (mm) 1 week from emergence (at age = 1 week)
λ_A fork length (mm) at 52 weeks from emergence (at terminal age A)
$\varepsilon_{h,i}$ age-0 mortality deviations by habitat type and block of weeks between sampling intervals

Estimated parameters for observation model

η coefficient of variation (CV) in length-at-age
π_h probability of capture for fish large enough to be fully vulnerable
ψ_h fork length (mm) where capture probability is reduced to 50% of the maximum (π_h)
τ_h standard deviation (inverse of slope) of capture probability – fork length relationship (mm)

PERSPECTIVE / PERSPECTIVE

Data weighting in statistical fisheries stock assessment models

R.I.C. Chris Francis

Abstract: The conclusions drawn from fisheries stock assessment models can depend strongly on the relative weights assigned to different data sets. However, there is no consensus amongst practitioners as to the best approach to data weighting. From a discussion of some key questions concerning data weighting in stock assessment models, I draw three guiding principles: (*i*) do not let other data stop the model from fitting abundance data well; (*ii*) when weighting age or length composition data, allow for correlations; and (*iii*) do not down-weight abundance data because they may be unrepresentative. I propose an approach to data weighting based on these principles. Two factors that complicate this approach are that some decisions are inevitably subjective (which underlines the need for expert knowledge in stock assessment), and some technical problems are unresolved.

Résumé : Les conclusions tirées des modèles d'évaluation des stocks des pêches dépendent fortement des poids relatifs attribués aux différents ensembles de données. Il n'y a cependant aucun consensus entre les utilisateurs sur la meilleure manière de pondérer les données. Une discussion de quelques-unes des questions principales sur la pondération des données dans les modèles d'évaluation des stocks me permettent de tirer trois principes directeurs: (*i*) ne pas permettre à d'autres données d'empêcher le modèle de bien s'ajuster aux données d'abondance, (*ii*) en pondérant des données de composition en âge et en longueur, tenir compte des corrélations et (*iii*) ne pas assigner une pondération inférieure à des données d'abondance parce qu'elles ne seraient pas représentatives — la méthodologie de pondération des données proposée ici est basée sur ces principes. Deux facteurs compliquent cette approche: certaines décisions sont inévitablement subjectives (ce qui souligne la nécessité d'obtenir des opinions d'experts dans l'évaluation des stocks) et certains problèmes techniques restent irrésolus.

[Traduit par la Rédaction]

Introduction

Most model-based fisheries stock assessments use multiple data sets. Thus one decision that must be made, explicitly or implicitly, during an assessment is how much weight to assign to each data set. This can be important because the estimated status of the stock being assessed will depend, possibly strongly, on these weights. Although there is wide agreement that data weighting is important (National Research Council 1998; Breen et al. 2003; Hulson et al. 2008), there seems to be no consensus amongst stock assessment practitioners as to how it should be addressed. Reports on individual stock assessments (mostly unpublished) often devote considerable space to data weighting, but there is wide variation amongst these reports in the methods used to weight different data sets. In this paper I discuss the main issues involved in data weighting in a stock assessment setting, and propose an approach to this problem. The topic is not straightforward because, as I will try to show, there is no satisfactory objective method of data weighting, and there are a number of unresolved questions concerning technical details of weighting schemes. Nevertheless, I think it is possible to develop some useful guiding principles, which are based as much on pragmatism and experience as on statistical theory. Before describing these principles, and a proposed approach to the problem, I will define some terminology and discuss some key data-weighting questions. The more technical details are given in two appendices.

Notation and terminology

In understanding the notation and terminology used below (Table 1), it is useful to view the stock assessment task at a series of levels of increasing complexity. At the simplest

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Table 1. Notation used in discussing and defining data weighting.

Type	Symbol	Description
Vector	$\boldsymbol{O}$	Vector of all data (observations) that are fitted to in a stock assessment model
	$\boldsymbol{P}$	Vector of all parameters being estimated in a stock assessment model
Function	L	Either the objective function in a stock assessment model or, if subscripted, the component of that objective function associated with an individual data point (in the latter case, L represents a negative log-likelihood)
Variable	O	An individual data point (observation) (e.g., a survey biomass estimate, or the proportion of the catch from a given year that is of a given age)
	E	The model's expected value for an individual data point
	T	The true (real world) value for an individual data point
	m	The number of individual data points in a data set
	m_{year}	The number of years covered by an abundance or composition data set
	m_{bin}	The number of bins in a composition data set
Subscript	i	Indexes the abundance data sets used in a stock assessment model
	j	Indexes the composition data sets used in a stock assessment model
	y	Indexes the years within an abundance or composition data set
	b	Indexes the bins within a composition data set (these bins may be defined by age or length, possibly in combination with sex)
Weighting parameters		
	λ, w	Simple weights
	c	Coefficient of variation (CV) used in weighting data
	σ	Standard deviation (SD) used in weighting data
	N	Multinomial sample size used in weighting data

level, this task involves fitting our data (contained in the vector $\boldsymbol{O}$) to a model by estimating the "best" values for those model parameters (in the vector $\boldsymbol{P}$) whose values are not known, where the best values are defined as being those that minimize our objective function L($\boldsymbol{O}$, $\boldsymbol{P}$). There are likely to be three main types of parameters in $\boldsymbol{P}$: (*i*) those that determine the historical dynamics of the fish population (e.g., the biomass of the unfished population, the recruitment in each year, and parameters for natural mortality and growth); (*ii*) those that describe the action of the fishery (e.g., the fishing mortality in each year, and the age at which fish are 50% selected in a particular fishery); and (*iii*) those from the error distributions for the data (e.g., a standard deviation (SD), or coefficient of variation (CV), for an abundance index). Our focus will be on type *iii* parameters, which affects data weighting.

Looking at the data in more detail, we will, for the most part, consider only two types of data: (*i*) observations (or estimates) of abundance (in biomass or numbers), and (*ii*) observations of the length or age composition of the catch from a fishery or a survey. These are the dominant, and often only, types of data used in stock assessments, and thus the most important in discussions of data weighting (other data types are discussed briefly below). We will think of the data vector as being made up of a number of data sets, each of which consists of a collection of individual data points, which are written as O_{iy}, for abundance data, or O_{jby}, for composition data. For example, one abundance data set might consist of estimates of (relative or absolute) abundance from a series of trawl surveys, with each individual data point being an abundance estimate for one of the survey years. In a typical composition data set, the individual data point is an estimate of the proportion of the catch for a given year that lies in a given length or age bin (bins may be defined by combinations of sex and age or length). If there are several fisheries, there may be one composition data set for each fishery; there may also be composition data sets associated with surveys.

Now, looking more closely at the objective function, this may be written as follows:

$$\text{(1)} \qquad \mathrm{L}(\boldsymbol{O}, \boldsymbol{P}) = \sum\nolimits_{iy} \mathrm{L}_{iy}(O_{iy}, \boldsymbol{P}) + \sum\nolimits_{jby} \mathrm{L}_{jby}(O_{jby}, \boldsymbol{P}) + \text{other terms}$$

I will consider only those stock assessments that use "statistical" models, like those typically developed using computer packages such as Stock Synthesis (NOAA 2011), CASAL (Bull et al. 2008), A-SCALA (Maunder and Watters 2003), Gadget (Begley 2005), or ADMB (ADMB Foundation 2011). I explicitly mean to exclude methods such as Virtual Population Analysis, and its descendents (e.g., Pope 1972; Shepherd 1999), in which composition data are treated as observed without error, and so not subject to data weighting. In statistical models, we can ignore the "other terms" (which might include penalty functions and, if the assessment is Bayesian, prior distributions) because they are not relevant to the question of data weighting. Our focus is on the functions L_{iy} and L_{jby}, which for these models are negative log-likelihoods, i.e., they describe the assumed error distribution for each data point. Many different error distributions have been used in stock assessment models but, all the common examples are expressed in terms of the expected value for the observation (E_{iy} or E_{jby}, which are functions of the parameters in $\boldsymbol{P}$) and a weighting parameter (see Table 2). The assumed (or estimated) values of weighting parameters determine how much weight is given to each data point. Thus, for example, if we assume a "normal by CV" error distribution for an abundance data point (T2.2 in Table 2) we can assign high

Table 2. Examples of negative log-likelihoods (ignoring constant terms) used in stock assessment models for abundance (O_{iy}) or composition (O_{jby}) data, showing the parameter that is used to weight each data point and the sense in which this parameter works (i.e., does a high weighting parameter value imply a high weight (+) or a low weight (–)).

		Weighting		
	Negative log-likelihood (L_{iy} or L_{jby})	Description	Parameter	Sense
T2.1A	$\lambda_{iy}(O_{iy}-E_{iy})^2$	Weighted sum of squares	λ_{iy}	+
T2.1B	$\lambda_{jby}(O_{jby}-E_{jby})^2$	Weighted sum of squares	λ_{jby}	+
T2.2	$\log(c_{iy}E_{iy})+0.5\left(\frac{O_{iy}-E_{iy}}{c_{iy}E_{iy}}\right)^2$	Normal by CV	c_{iy}	–
T2.3	$\log(\sigma_{iy})+0.5\left(\frac{O_{iy}-E_{iy}}{\sigma_{iy}}\right)^2$	Normal by SD	σ_{iy}	–
T2.4A	$\log(\sigma_{iy})+0.5\left[\frac{\log(O_{iy}/E_{iy})}{\sigma_{iy}}+0.5\sigma_{iy}\right]^2$	Lognormal by CV[a]	c_{iy}[b]	–
T2.4B	$\log(\sigma_{jby})-\log\left\{\exp\left[-0.5\left(\frac{\log(O_{jby}/E_{jby})}{\sigma_{jby}}+0.5\sigma_{jby}\right)^2\right]+0.01\right\}$	Robust lognormal	c_{jby}[c]	–
T2.5	$\log(\sigma_{iy})+0.5\left[\frac{\log(O_{iy}/E_{iy})}{\sigma_{iy}}\right]^2$	Lognormal by CV[a]	c_{iy}[b]	–
T2.6	$-N_{jy}O_{jby}\log E_{jby}$	Multinomial	N_{jy}	+
T2.7	$0.5\log(E'_{jby})-\log\left\{\exp\left[\frac{-(O_{jby}-E_{jby})^2}{2E'_{jby}/N_{jy}}\right]+0.01\right\}$	Robust multinomial[d]	N_{jy}	+

[a] The difference between the two lognormals is that in T2.4A, it is assumed that the expected value of O_{iy} is E_{iy}, whereas in T2.5 the expected value of $\log O_{iy}$ is assumed to be $\log E_{iy}$;

[b] $c_{iy}=\sqrt{\exp(\sigma_{iy}^2)-1}$

[c] $c_{jby}=\sqrt{\exp(\sigma_{jby}^2)-1}$

[d] $E'_{jby}=(1-E_{jby})E_{jby}+0.1/m_{bin,j}$

(or low) weight to that observation by setting c_{iy} to be low (or high). Another way of thinking of this is that the weight we assign to an observation O_{iy}, is determined by how close we expect it to be to the model's expected value, E_{iy}; a high weight means O_{iy} is expected to be close to E_{iy} (so its CV will be small). Any adjustment of weighting parameters that gives more (or less) weight to a data set is said to up-weight (or down-weight) that data set.

It is important to understand that some sorts of information used in stock assessments are not "data", in the sense used in this paper, and thus not relevant to discussions of data weighting. For example, a set of age and length measurements on individual fish may be used outside the assessment model to estimate growth parameters (such as von Bertalanffy coefficients), which are then treated as fixed parameters in the model. In this case, neither the age–length measurements nor the growth parameters should be thought of as data, and thus subject to weighting. The age–length measurements would be considered as data only if they appeared in the objective function (in which case the growth parameters would be estimated within the model). Another type of information that I will not treat as data, and thus subject to weighting, is that used in a Bayesian model to construct a prior distribution for a model parameter. I will also ignore the parameter, common to many assessment models, that describes the degree of year-to-year variation in recruitment (e.g., the parameters σr of McAllister and Ianelli 1997; and λF of Savereide and Quinn 2004) because although it looks, mathematically, like a data-weighting parameter, it does not actually serve to weight any data set.

For readers interested in technical details, there are three points to be made about the examples in Table 2. First, some of the terms in the negative log-likelihoods may be considered optional. For example, many authors omit the $\log(\sigma_{iy})$ term in examples T2.3–T2.5. This is appropriate if, as is often true, the parameter σ_{iy} is assumed to be known; but it is inappropriate if σ_{iy} is to be estimated. Second, the weighted sum of squares (examples T2.1A, T2.1B) is not a negative log-likelihood, but it is included here because its use is not uncommon (e.g., Taylor et al. 2007; Hulson et al. 2008), and it may be interpreted as a "normal by SD" negative log-likelihood simply by setting $\sigma_{iy}=\sqrt{0.5/\lambda_{iy}}$ (for T2.1A), or $\sigma_{jby}=\sqrt{0.5/\lambda_{jby}}$ (for T2.1B). Third, for examples T2.4A, T2.4B, and T2.5 we have a choice in weighting parameters between the SDs in log space (σ_{iy} or σ_{jby}) and CVs in natural space (c_{iy} or c_{jby}). I have chosen the latter because they are more easily interpretable.

Two-stage weighting

It is common practice to weight some or all data sets in two stages. Stage 1 weights are devised before the model is run, and generally use information about the way in which the data were collected (i.e., sample sizes and structures). It is not uncommon for each data point to have a different weight. Stage 2 weighting occurs after the model has been run (or sometimes during a model run), and is intended to make the data weights more consistent with the model output. The weighting adjustments at stage 2 usually apply to whole data sets, rather than individual data points, using formulations like those in Table 3. For example, if equation T3.4 (Table 3) is used for composition data, then before the model is run, the stage 1 weights, $\tilde{N}_{jy}$, will be fixed and provisional values will be assigned to the stage 2 weights, w_j. The assessment model is then run, information from that run

Table 3. Examples of equations that allow, for the example negative log-likelihoods of Table 2, two-stage data weighting.

	Equation	Corresponding example(s) in Table 2	Weighting parameters	
			Stage 1	Stage 2
T3.1	$\lambda_{iy} = \tilde{\lambda}_{iy} w_i$	T2.1A	$\tilde{\lambda}_{iy}$	w_i
T3.2	$c_{iy} = \tilde{c}_{iy}/w_i$	T2.2, T2.4A, T2.5	$\tilde{c}_{iy}$	w_i
T3.3	$\sigma_{iy} = \tilde{\sigma}_{iy}/w_i$	T2.3	$\tilde{\sigma}_{iy}$	w_i
T3.4	$N_{jy} = \tilde{N}_{jy} w_j$	T2.6, T2.7	$\tilde{N}_{jy}$	w_j
T3.5	$c_{iy} = \sqrt{\tilde{c}_{iy}^2 + c_i^2}$	T2.2, T2.4A, T2.5	$\tilde{c}_{iy}$	c_i
T3.6	$c_{jby} = \sqrt{\tilde{c}_{jby}^2 + c_j^2}$	T2.4B	$\tilde{c}_{jby}$	c_j
T3.7	$\sigma_{iy} = \sqrt{\tilde{\sigma}_{iy}^2 + \sigma_i^2}$	T2.3	$\tilde{\sigma}_{iy}$	σ_i
T3.8	$N_{jy} = 1/[(1/\tilde{N}_{jy}) + (1/N_j)]$	T2.6, T2.7	$\tilde{N}_{jy}$	N_j

Note: The tilde (~) above the symbol for a weighting parameter indicates that it applies to stage 1.

is used to adjust the stage 2 weights, and the model is run again with the adjusted weights. The process of adjusting the weights may be applied several times until the weights reach stable values (this is called iterative reweighting).

Some key data-weighting questions

Answers to the questions addressed in this section will help to set the scene for the rest of the paper.

Why is data weighting important?

The main reason that data weighting is important in stock assessments is that it can substantially change the results of the assessment. This can sometimes be demonstrated by constructing a profile on a key parameter (called a likelihood profile if estimation is by maximum likelihood, or a posterior profile if it is Bayesian; as illustrated in Fig. 1) (a profile is constructed by refitting the assessment model many times, each time with a different fixed value of the chosen parameter – unfished biomass, B_0, in this case). In this example, the profile shows that that the abundance data (a single time series of trawl survey biomass estimates) were best fitted when B_0 was 42 000 t; the composition data (proportions at age in catches from the survey and two fisheries) were best fitted at B_0 = 80 000 t; and in this assessment the data have been weighted in such a way that the model estimate of B_0 (44 840 t) is quite close to the best estimate from the abundance data. Data weighting was important in this assessment because the estimate of B_0 could have taken any value between 42 000 t and 80 000 t, depending on the relative weights assigned to the biomass and composition data. Also, the estimated current biomass (a key management indicator in New Zealand stock assessments) could have taken any value between 44% B_0 and 57% B_0, depending on the data weighting (Fig. 1*b*).

Another reason that data weighting is important in stock assessments is that it affects all the usual tools of statistical inference that are used in these assessments (Deriso et al. 2007). For example, we may want to use the Akaike Information Criterion (AIC; Akaike 1974) to decide which of two alternative equations for a selectivity curve is most consistent with our data, or to test the hypothesis that a fishery selectivity has changed in recent years. The decisions we make in these cases may be affected by a change in data weighting. Also, any estimated confidence (or credibility) intervals for parameters (or for derived quantities, like current biomass) will change when data weightings are changed.

Why is stage 2 weighting necessary?

There is an argument that says that we ought to be able to do without stage 2 weighting. After all, correct weighting requires knowledge of the error distribution of our observations, and many types of data allow us to estimate that error distribution before we start modelling. This appears to be the argument behind the claim by Maunder (2003, p. 470) that weighting factors are not needed in what he calls "the new integrated analysis."

The argument is wrong because it doesn't recognise that there are three types of error to consider (Fig. 2). These arise because for any quantity we observe for our stock assessment (e.g., a biomass, or a proportion at age in a given year) there are three different values: (*i*) the value we observe, *O*; (*ii*) the value expected by our model, *E*; and (*iii*) the true (real world) value, *T*. *O* differs from *T* because of observation error, which is the error whose distribution, and likely size, we may be able to infer from our data (some ways of doing this are discussed below). *E* differs from *T* because of process error, by which I mean all the ways in which our model is only an approximation to the real world. The error we are interested in (i.e., that described in our negative log-likelihoods) is that between *O* and *E*. I call this total error because it is the sum of observation error and process error.

This characterization of errors gives an obvious interpretation to the two stages of data weighting. At stage 1, we assign the weights (or CVs) appropriate for observation error; at stage 2, we adjust those weights to allow for process error. This adjustment is usually done either multiplicatively (as in eqs. T3.1–T3.4 of Table 3) or additively (as in T3.5–T3.8). Note that when we add a process error with CV c_{proc} to an observation error with CV c_{obs}, the total error has CV $\sqrt{c_{\text{proc}}^2 + c_{\text{obs}}^2}$ (assuming the errors are independent, which

Fig. 1. Results from a profile on unfished biomass, B_0, in the New Zealand hake assessment of Horn and Francis (2010): (*a*), the (total) objective function (solid line), and the components of it associated with abundance (dashed line) and composition data (dotted line), (all zero-adjusted), with plotted points showing the minimum for each curve; and (*b*), the relationship between B_0 and current biomass in the profile.

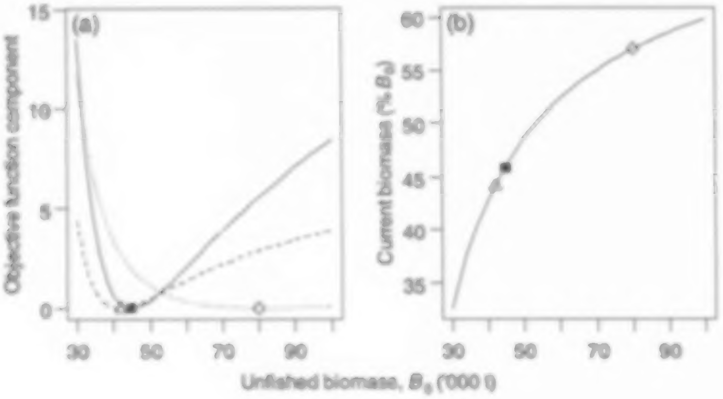
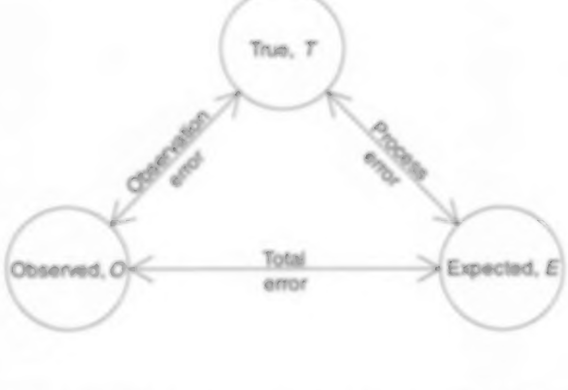


Fig. 2. Schematic illustration of the three types of error that exist between the three values of any quantity of interest (such as a biomass or proportion at age): the observed value, *O*; the true (real world) value, *T*; and the value *E* expected by our stock assessment model.



seems reasonable, given their sources). A similar logic applies to equation T3.8: if both *O* and *E* are multinomially distributed, with parameters (N_{obs}, T) and (N_{proc}, T), respectively, then the variance of $(O - E)$ is the same as that of a multinomial distribution with parameters (N_{total}, T), where $N_{total} = 1/[(1/N_{obs}) + (1/N_{proc})]$.

To avoid stage 2 weighting we must be able to estimate the likely size of both observation and process error for all our data before we run our model. I will show that it is possible to do this for some types of abundance data, but never for composition data. Thus, stage 2 weighting will always be necessary, at least for composition data.

Can we estimate process error outside the stock assessment model?

The answer to this question is yes for some types of abundance data, but no for composition data.

Several studies have attempted to estimate the process error associated with trawl survey biomass data by comparing the estimated observation errors with the sizes of the residuals when these biomass estimates are used in a stock assessment model. Pennington and Godø (1995) analysed four survey time series and concluded that the variance of the total error was approximately twice as large as that of the observation error (i.e., process and observation error were approximately equal in variance). Francis et al. (2003) took a different approach, assuming that the CV of the process error was the same for each of 18 trawl-survey time series, and estimated that a process error CV of about 0.2 would be needed to best explain the size of the stock assessment residuals. These two results are broadly similar because the mean observation-error CV in the latter study was 0.22. Both studies assumed that the main source of this process error was year-to-year variation in survey catchability, although this assumption was not necessary for their analyses. A third study, by Millar and Methot (2002), focussed primarily on between-species variation in mean catchability for six species of rockfish caught in a triennial series of eight trawl surveys off the west coast of the US. However, they also estimated year-to-year changes in catchability (assumed to be the same for all species), which suggest a process error CV of about 0.35 for this survey (this is the approximate CV, in natural space, of the midpoints of the distributions in Millar and Methot 2002's Fig. 5). This CV may be atypically high for research surveys because this particular survey series uses chartered commercial vessels and, as noted by Millar and Methot (2002), it is not possible to use the same vessels and skippers each time.

For acoustic survey biomass estimates there are several factors whose year-to-year variation has been identified as contributing to process error. These include mean target strength, the abundance of nontarget species, the proportion of the target population that is not detectable (because it is too close to the sea floor), and the timing of the survey relative to that of spawning activity. As long as the likely scale of amongst-survey variation is known for each factor, it is possible to estimate the extent of process error using a simulation procedure (Rose et al. 2000; O'Driscoll 2004).

Process error in composition data is much more complex because it occurs in two dimensions (time and age or length), or sometimes three (if the data are sex-specific). The model assumptions that contribute most to this error are those associated with natural mortality and selectivities. For example, in many assessments (including that associated with Fig. 1) it is assumed that natural mortality is independent of both age and time, and fishery selectivities do not vary with time. In principle, we could use a simulation approach, similar to that used for acoustic surveys, to estimate the distribution of process error arising from the failure of these (or other similar) assumptions. This does not work in practice because we do not know how wrong the assumptions are (e.g., we do not know the scale of year-to-year variations in natural mortality, or how this scale varies with age). Thus it is not realistic to try to estimate the process error in composition data outside the stock assessment model.

Why abundance data should have primacy?

Some approaches to data weighting treat all data types in the same way. I suggest that this is a mistake, and that primacy should be given to abundance data, by which I mean that special attention should be devoted to ensuring that the abundance data are well fitted by the model. My reasons for this have to do with the purposes of stock assessment modelling.

Most of the key questions we address in stock assessments are to do with abundance. We want to know what is the current stock abundance (usually relative to historical levels, or to the unfished abundance), and whether it is increasing or decreasing. We might also want to know what the effect of possible future levels of fishing is likely to be, and we will express this effect in terms of biomass trends (rates of increase/decrease). Another quantity of interest is some measure of fishing pressure (usually either an instantaneous rate of fishing mortality, or a catch/biomass ratio) which, of course, is directly related to abundance (for a given catch, the greater the abundance is in any given year, the lower the fishing pressure must have been). We should give primacy to abundance data because they provide direct information about the stock assessment quantities that are of most interest, whereas composition data provide only very indirect information about these quantities. If we do not grant this primacy, then there is a danger that any signal from abundance data will be swamped by that from composition data, simply because the latter data type is typically much more numerous (in terms of individual data points).

It is easy to be misled by plots like Fig. 1, which suggest that composition data contain much useful information about abundance. The point to remember is that the likelihood calculations that produced this plot depend on very strong assumptions, which we know to be false, but which we need to make to have a useful stock assessment model. In this model it was assumed that natural mortality was independent of age and year, and that the selectivities of the two fisheries did not vary by year. Such assumptions are useful in allowing us to infer average selectivity curves for the survey and fisheries, and which year classes are particularly strong or weak. However, it seems to be a mistake to rely on them in making abundance inferences from composition data. In this particular assessment we would see the weakness of such inferences if we were to add a separate line in for each of the three composition data sets to Fig. 1. These additional lines (not plotted) would show that these data sets are inconsistent in their (apparent) abundance signal: the line for the catch at age data from one of the fisheries would have its minimum at the lowest value of B_0 (30 000 t), whereas for both the survey and the other fishery the minimum would be at the highest value (100 000 t).

The situation to avoid, is one in which the relative weighting given to composition data causes a poor fit to the abundance data. We should accept such a fit only if we are confident that the composition data provide clear evidence of abundance trends that differ from those suggested by our abundance data. This, I suggest, will be a rare occurrence. We rely on composition data to tell us about strong and weak year classes and the shape of selectivity curves, not about abundance trends.

How should we deal with abundance data that may be unrepresentative?

It is not uncommon in stock assessment documents and meetings for doubt to be expressed as to whether an abundance data set is representative, i.e., whether the trend in that data set is actually the same (allowing for observation error) as that in the population being assessed. For example, a catch per unit effort (CPUE) data set will be unrepresentative if it is from a fishery in which CPUE is not related to abundance. Survey estimates that cover only a part of the population will be unrepresentative if the population fraction covered by the survey is very different in different years. If two abundance data sets are clearly contradictory (i.e., they show very different trends over the same years) then at least one of them is likely to be unrepresentative.

It may seem reasonable to down-weight data sets that may be unrepresentative, but this is a bad idea. A better response is to consider alternative assessments in which possibly unrepresentative data sets are omitted. Thus, if there is only one suspect data set we should produce two assessments: one including this data set, and the other excluding it. These two assessments correspond to the two logical possibilities: A, the data set is representative; or B, it is not. An important uncertainty that must be communicated to fishery managers is that although only one of the two assessments is likely to be correct, we do not know which one. If we simply down-weight the suspect data set we will produce a result that lies somewhere between these two assessments. This result will be wrong in case A, and it will be wrong in case B, and we will not have alerted fishery managers to the possibility that one data set is unrepresentative. Both Richards (1991) and Schnute and Hilborn (1993) made a similar point when discussing the problem of contradictory data sets in stock assessments. In this case it is important to acknowledge the uncertainty about which data set is unrepresentative; a single assessment using all data sets is likely to be wrong, no matter which of the data sets turns out to be unrepresentative (Schnute and Hilborn (1993) describe a likelihood that allows both contradictory data sets to be used in the same assessment and also acknowledges the uncertainty about which one is unrepresentative, but this seems to me to be an elegant way of demonstrating the problem, rather than a practical way of dealing with it in actual assessments).

Sometimes there will be clear evidence that an abundance data set is unrepresentative. For example, consider an abundance index that is initially stable and then suddenly increases (or decreases) sharply. This would clearly be unrepresentative in a fishery in which catches were stable and there was no evidence of extreme (very strong or weak) year classes. Data sets believed to be unrepresentative should be discarded; they certainly should not be retained and downweighted.

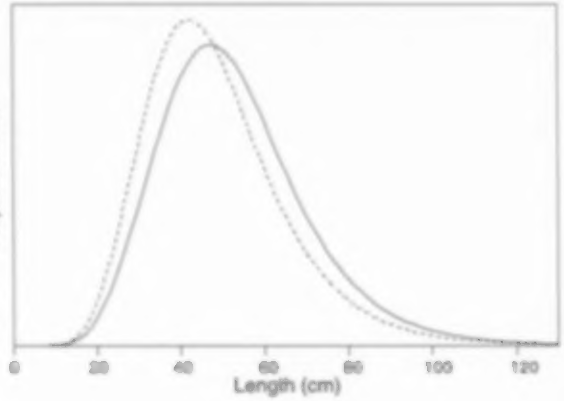
How should we deal with correlations in composition data?

It is commonly observed that fish in the same catch (e.g., from the same tow of a trawl net, or the same set of a longline) tend to be more similar to each other in length or age than are fish from different catches. Pennington and Vølstad (1994) called this intrahaul correlation. Sometimes this correlation can occur at a higher level, with fish caught by the same vessel, in a multiple-catch fishing trip, being more alike than fish caught by different vessels (e.g., see Fig. 10 of Francis 2006). These phenomena can induce substantial correlations in age or length composition data sets that are constructed from samples from multiple catches (whether from surveys or fisheries). The proportions O_{jby} and $O_{jb'y}$ will tend to be positively correlated if the bins b and b', are close together, and negatively correlated if they are distant (e.g., see Fig. 12 of Francis 2006). A very similar pattern was shown in Fig. 1 of Hrafnkelsson and Stefánsson (2004), although they were plotting different, but related, correlations (those between the length frequencies at different survey stations, rather than within the overall length frequency from a survey). These correlations are much bigger than those that always occur amongst multinomial proportions (the latter, which are caused by the fact that the proportions for each year must sum to 1, are always negative and usually small, having the following value: $-[E_{jby}E_{jb'y}/(1 - E_{jby})(1 - E_{jb'y})]^{0.5}$).

The effect of these correlations is to reduce the amount of information in composition data sets. This was demonstrated by Pennington and Vølstad (1994), who analysed length frequency data for haddock in 26 trawl surveys on Georges Bank. For each survey they calculated what they called the effective sample size: the number of fish that would be required, in a simple random (i.e., uncorrelated) sample from the population, to estimate the population mean length with the same precision as was achieved in the survey. Over the 26 surveys, the median effective sample size was 21, which was half the median number of tows that caught haddock, and only 2.5% of the median number of fish measured (these numbers come from Table 1 of Pennington and Vølstad 1994). In a similar analysis, based on trawl surveys conducted in the Barents Sea, off Namibia, and off South Africa, Pennington et al. (2002) found that the effective sample size for each survey was, on average, about the same as the number of tows.

The correlations discussed so far are part of the observation error for composition data, but there is also likely to be correlation in the process error. Consider, for example, a stock assessment in which a fishery selectivity is assumed to be constant, but actually varies from year to year. In a year in which the fishery happens to target larger (or older) fish than usual, the selectivity curve will be shifted to the right, compared with that expected in the model, and so will the observed length (or age) frequency from the catch (Fig. 3). Notice that the residuals $(O_{jby} - E_{jby})$ are all negative for the smaller lengths (up to about 48 cm), and all positive for the greater lengths (Fig. 3). This pattern would be reversed in a year in which the selectivity curve was shifted to the left. Thus, this year-to-year shifting of the selectivity would induce the same type of correlations in the process error for the proportions at length as was described above for the observation error (i.e., positive correlations between bins that are close together, and negative correlations for distant bins). Other types of process error would produce a similar effect (e.g., year-to-year variation in the natural mortality on small fish – perhaps caused by fluctuations in their food supply).

Fig. 3. Illustration of the relationship between the observed (solid line) and expected (broken line) catch length frequencies in a year in which the true fishery selectivity is shifted to the right of that assumed in the stock assessment model.



How should we take account of the correlations associated with composition data sets? There are three possible approaches, none of which is completely satisfactory. The first, and most common approach, is to ignore the correlations (i.e., to act as if they were zero). A simple error model is used for the composition data (e.g., T2.4B or T2.6 in Table 2), and some method that assumes zero correlations is used to set weights at stages 1 and 2. Some of the many variants of this approach are described in Appendix A. The danger with this approach is that the composition data sets are likely to be over-weighted (remember that correlations tend to reduce the amount of information in composition data, and less information should mean less weight), and this could cause poor fits to abundance data. The second approach is to use a complicated error model with an appropriate correlation structure. One problem with this approach is that although there have been several attempts to model observation error in composition data (e.g., Kvist et al. 2001; Hrafnkelsson and Stefánsson 2004; Miller and Skalski 2006) we have no way of knowing whether these will be appropriate for total (i.e., observation + process) error. Another problem is that these error models typically require many more

Table 4. Final (stage 2) multinomial sample sizes, estimated using four alternative methods of calculation (TA1.1, TA1.2, TA1.3, TA1.8; see Appendix A for details), for four age composition data sets with multinomial errors (and assumed sample size 150) in one model run from the 2006 assessment of southern hake (*Merluccius australis*) in Chile.

	Estimated sample size			
Composition data set	TA1.1*	TA1.2*	TA1.3*	TA1.8†
Trawl fishery	258	115	116	15
Commercial longline fishery	240	154	152	10
Artisanal longline fishery	557	251	248	25
Survey	338	232	233	69

*These methods do not allow for correlations.

†This method allows for correlations.

parameters than the simple models. I am not aware of any assessments using this second approach. I favour the third approach, which is to use simple error models, but to allow for correlations by using a data-weighting approach analogous to the method of Pennington and Vølstad (1994) for calculating effective sample sizes. That is to say, the weights (in the form of CVs or multinomial sample sizes) are calculated so as to be consistent with the size of the errors in mean length (for length composition data) or mean age (for age compositions) (see Appendix A for details of three methods using this approach).

To see the effect of allowing for correlations, consider a model run from the 2006 assessment of southern hake (*Merluccius australis*) in Chile, in which there were four age composition data sets, all of which were assumed to have a multinomial error distribution with sample size 150 (the same for all years). If we use stage-2 weighting methods that ignore correlations, the resulting adjusted sample sizes are mostly greater than 150 (see columns 2–4, Table 4), suggesting that insufficient weight was given to the composition data sets in this model. However, when we allow for correlations, the adjusted sample sizes are all much smaller than 150 (last column, Table 4), implying that the composition data were over-weighted. This pattern is not uncommon; multinomial sample sizes calculated with allowance for correlations are usually much smaller than those in which correlations are ignored. An effect of the correlations is illustrated (Fig. 4). Although there is broad agreement between the observed mean ages and those expected from the model (in that both show an overall decline), the expected values are mostly outside the 95% confidence intervals for the observed values. In other words, year-to-year variation in the age composition data was much greater than is consistent with a simple random sample size of 150 (as was assumed in calculating the confidence intervals). Use of this sample size implies that these data sets contain more information than they really do.

I should emphasise that my preference for stage-2 weighting methods based on errors in mean length or age is not based on any statistical theory supporting these methods. It is simply a pragmatic response to (*i*) the fact that the commonly used methods are based on an assumption (of uncorrelated residuals) that is demonstrably wrong; and (*ii*) the empirical observation (in plots like Fig. 4) that these methods give too much weight to composition data.

How can robust likelihoods help?

Robust likelihoods are particularly important for composition data because they help to avoid the situation in which the model fit is driven by a small number of composition data points that are extreme outliers. These likelihoods allow a better fit to the majority of composition data points and reduce the probability that the composition data will prevent good fits to abundance data.

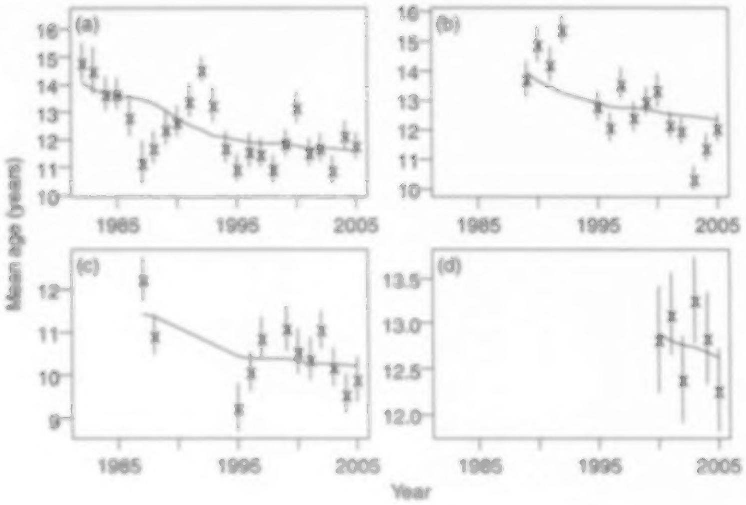
Fournier et al. (1990) pointed out that standard maximum-likelihood methods can perform poorly when applied to length composition data because they are too sensitive to the deviations from the model's hypotheses (i.e., process error) that are common with such data. They devised a robust alternative to the multinomial likelihood (T2.7 in Table 2: I have called this a robust multinomial because of the way it is parameterised, but technically it is a robust multivariate normal), which is used in MULTIFAN-CL (Fournier et al. 1998), a stock assessment program used for many tuna stocks. [In the original version of the robust multinomial, the term N_{jy} was replaced by min(N_{jy}, 1000); I omitted this here because I think it will rarely be used in stock assessments with effective stage 2 weighting]. A modification of T2.7, in which $E'_{jby} = (1 - O_{jby})O_{jby} + 0.1/m_{bin,j}$, is available in some programs (e.g., Maunder and Watters 2003; Bull et al. 2008) following the finding by Starr et al. (1999) that the original likelihood can produce biased estimates. An approach similar to that of Fournier et al. (1990) was used to make a robust lognormal (T2.4B in Table 2) that is available in CASAL (Bull et al. 2008).

Proposed approach to data weighting

From the questions discussed above I derive three principles and an end point to aim for in addressing the problem of data weighting in stock assessments. Principle 1: Do not let other data stop the model from fitting abundance data well. Principle 2: When weighting composition data, allow for correlations. Principle 3: Do not down-weight abundance data because they may be unrepresentative.

From a data-weighting point of view, the ideal end point of a stock assessment is a single assessment model in which

Fig. 4. Observed (×) and expected (curved line) mean age for the four age composition data sets in the stock assessment of Table 4: (*a*) commercial trawl; (*b*) commercial longline; (*c*) artisanal longline; and (*d*) survey. The vertical lines are 95% confidence intervals for mean age, calculated assuming simple random sampling with sample size 150 in each year.



all abundance data sets are fitted well. This may not be possible when there are conflicts amongst the data sets. In that case, we should aim for a set of alternative assessment models, in each of which one or more data sets has been omitted but all remaining abundance data sets are well fitted. The following approach to data weighting is intended to achieve this desired end point while respecting the above three principles.

Weighting abundance data

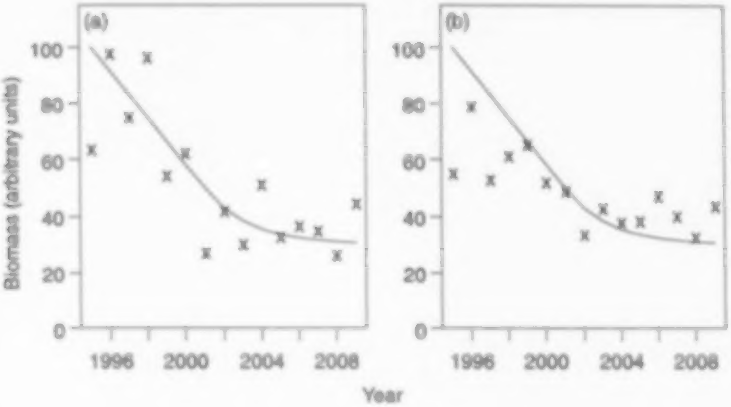
To apply Principle 1, we must have some idea, before we run the stock assessment model, of how we are going to decide whether the model has fitted the abundance data well. That is to say, we need to know how large the CVs (or SDs) of the total errors for these data sets should be. I have described above some methods for estimating these total CVs for trawl and acoustic indices. For other abundance data sets, I suggest using the approach adopted by Clark and Hare (2006, p. 9) for a CPUE data set: use the CV of the residuals of the fit of a data smoother to the abundance data (this is equivalent to saying that we expect the stock assessment model to fit these data as well as the smoother). These total CVs should be applied at stage 1 (i.e., before the model is run). They should not be adjusted at stage 2, because they have already been set to reflect our expectations as to how well the model should fit these data.

Weighting other types of data

For composition data, I suggest using robust likelihoods (e.g., T2.4B or T2.7 from Table 2), to reduce the influence of extreme outliers, and setting the initial (stage 1) weights to represent the approximate size of observation errors. Because these initial weights will be adjusted, often substantially, with stage-2 weighting, their relative sizes (within data sets) are more important than their absolute sizes. For example, it is important that years with poorer sampling of the catch be given less weight than those with better sampling. The weighted sum of squares (T2.1B in Table 2) should be avoided for composition data, because it implies that for a proportion p, CV(p) ∝ $1/p$, whereas the more typical pattern is that for a multinomial proportion, i.e., CV(p) ∝ $\sqrt{(1-p)/p}$ (e.g., see Fig. 3, Crone and Sampson 1998). Because composition data typically derive from complex multistage samples, bootstrap resampling is an excellent (although computationally intensive) way of estimating observation-error CVs. Some other approaches have been suggested by Morton and Bravington (2008) and Robotham et al. (2008). If the (robust) multinomial distribution is preferred to the lognormal, a nonlinear regression (of CV on proportion) can be used to calculate the equivalent multinomial sample size from the bootstrap-estimated CVs (Crone and Sampson 1998). If these more complicated approaches are not possible, then I see little harm in the use of the (preferably robust) multinomial with sample sizes set by some ad hoc rule (e.g., Crone and Sampson 1998 estimated a relationship with number of trips sampled; Gilbert and Phillips 2003 set sample sizes to be 5× the number of landings sampled; Maunder and Watters 2003 used number of wells sampled; see also the discussion of length composition sample sizes in Thompson et al. 2009). I don't think it is important to allow for correlations (Principle 2) at stage 1.

Stage-2 weighting is important for composition data because it allows us to include process error, which cannot be estimated before the model is run, and thus avoid overweighting these data. Many different methods of stage-2 weighting have been proposed (see Appendix A). Those methods that allow for correlations are to be preferred, because they almost always produce smaller weights for the composition data (as in Table 4) and thus reduce the probability that these data will cause a poor fit to the abundance data (Principle 1).

Fig. 5. Demonstration that the standard deviation of the normalized residuals (SDNR) by itself is not a good measure of how well a model biomass trajectory (line) fits a set of biomass observations (×). The SDNR is exactly the same in both panels but the residual patterns indicate a good fit in panel (*a*), and a poor fit in panel (*b*).



One weakness of stage-2 weighting methods that allow for correlations is that they don't work well with data sets that cover few years. For example, if we have a 5-year composition data set with 20 age bins, the stage-2 weights from such methods are not well estimated, because they derive from just 5 mean-age errors, whereas those from most methods ignoring correlations (e.g., methods TA1.1–TA1.3) are based on the errors at 100 data points (or 200, if sex is included). It will sometimes be sensible to make inferences from other larger data sets. For example, if we find for our large composition data sets that the adjusted sample sizes with method TA1.8 are approximately 20%, say, of those calculated with TA1.1, then we might assume that this ratio is true for a small data set. Don't be concerned if the final weights for composition data are rather small. Recall the results quoted above from Pennington and Vølstad (1994) and Pennington et al. (2002), which show that effective sample sizes for length compositions can be very small (those for age compositions based on age-length keys tend, in my experience, to be larger). These small weights will reduce the chance that composition data will cause a poor fit to abundance data (Principle 1) and often do not greatly affect estimates of those parameters about which these data are most informative (year-class strengths and selectivity curves).

It is difficult to provide specific advice for data types other than abundance and composition, e.g., proportions mature by length (Taylor et al. 2007), and length increments from mark–recapture experiments (Breen et al. 2003). The only general point I would make is that Principle 1 should apply to these data.

Judging whether abundance data are well fitted

When we have completed stage 2 weighting and rerun the model with the adjusted weights, we should check whether the abundance data are well fitted. A common way to do this is to calculate, for each abundance data set, the standard deviation of the normalized (or standardized) residuals (SDNR) (Breen et al. 2003) (see Appendix B for methods of calculation). For an abundance data set to be well fitted, the SDNR should not be much greater than 1 (a value much less than 1, which means that the data set is fitted better than was expected, is not a cause for concern). What is meant by "much greater than 1" depends on *m* (the number of years in the data set). Since the normalized residuals are (approximately) normally distributed, a reasonable guideline is that the SDNR should be less than $[\chi^2_{0.95,m-1}/(m-1)]^{0.5}$, where $\chi^2_{0.95,m-1}$ is the 95th percentile of a χ^2 distribution with $m-1$ degrees of freedom (e.g., this means upper limits of 1.54, 1.37, and 1.26 for $m = 5$, 10, and 20, respectively).

Although an SDNR not much greater than 1 is a necessary condition for a good fit, it is not sufficient. It is important to plot the observed and expected abundances to be sure that the fit is good (Fig. 5).

What to do when abundance data are not well fitted

When an abundance data set is not well fitted by an assessment model, the first thing to check is whether Principle 1 is being violated. Can we get a good fit by either up-weighting the abundance data or down-weighting the composition (or any other) data? If so, this should be done. A point to note is that if, to achieve a good fit, an abundance data set is up-weighted, its SDNR after up-weighting should be calculated using the original weights (because these weights represent our best information about how well this data set should be fitted).

What should be done if the problem does not lie with the composition data? If there is only one abundance data set, then this should be considered unrepresentative (unless there is some acceptable way to modify the model structure to achieve a good fit), and thus discarded. If there are multiple abundance data sets, and one or more is not well fitted, then there is good reason to believe that at least one data set is unrepresentative (although not necessarily one of those that is not well fitted). The approach to take here is as outlined above in the section on unrepresentative data sets. Create a set of alternative models, in each of which one or more abundance data sets is omitted, and all the remaining abundance data sets are well fitted. The set of alternative models should be as small as possible. The point to note here is that we should not simply down-weight potentially unrepresentative data sets (Principle 3); instead we should investigate the effect of omitting them, or other data sets which may be in conflict with them. The aim is to present the set of alternative models to fishery managers and say that each one of these models could be true, but we don't know which one. It may be possible to use the expertise of people with knowledge of the data, and the fishery, to provide an indication as to which of the alternative models are more, or less, likely to be true.

Dealing with doubt about abundance data

Principles 1 and 3 should not be interpreted as suggesting that stock assessment scientists should ignore any doubts they may have about the representativeness of their abundance data. Nor do I want to suggest that it is easy to determine whether such data are representative. It is not. What I am advocating is that we deal with any doubt about the representativeness of a particular abundance data set by constructing an alternative model (or models) that omits that data set. Any model that includes this data set is intended to address the possibility that the data set *is* representative, so for this model we apply Principles 1 and 3. The model (or models) without this data set addresses the possibility that the data set is not representative.

Goodness of fit to composition data

The above data-weighting procedure does not involve checking whether the composition data are well fitted. This is because, in my experience, a poor fit to composition data is much more likely to be caused by poor model assumptions than by inappropriate data weights. For example, fits to fisheries composition data may be poor if the wrong selectivity curve is assumed (e.g., if a logistic selectivity is assumed when the actual selectivity is strongly domed). Note that SDNRs are not an appropriate measure of goodness of fit for composition data because the theory underlying them assumes that the errors are uncorrelated.

Discussion

This paper offers three aids to those dealing with the difficult problem of data weighting in fisheries stock assessments: (*i*) some guiding principles; (*ii*) an end to aim for; and (*iii*) a proposed approach to achieve that end. Of these, the last is least important. For many assessments, even a simple trial and error approach, as suggested by Fournier and Archibald (1982), may be adequate if it is aimed towards the end I have described, and supported by the guiding principles.

One source of difficulty in data weighting is that some of the decisions involved are inevitably subjective. For example, there is no objective way of deciding whether abundance data are adequately well fitted, or of setting the degree of smoothing to be used in setting CVs for abundance data sets. This necessity for subjective decisions underlines the importance of expert knowledge (concerning the fishery, the data, and the models) in stock assessment. I don't think the problem of subjectivity is sufficiently severe that we should abandon statistical population models, as advocated by Cotter et al. (2004).

Another difficulty is that there are still many unresolved technical problems. For example, should observation and process errors be combined multiplicatively (as in T3.1–T3.4) or additively (as in T3.5–T3.7)? It is unclear why method TA1.1 performs so differently from TA1.2 and TA1.3 in the example of Table 4, although the derivations of these methods show they are intended to achieve the same thing (see Appendix A). I know of only one approach to stage-2 weighting of composition data that allows for correlations (method TA1.8, with variants TA1.9 and TA1.10). If other researchers addressed the problem of devising such a method their approaches might be equally plausible, while producing quite different results. There is a need for a simple and plausible error distribution for composition data that allows for substantial correlations.

Even when the data-weighting approach described above appears to work well, and produces a single assessment model in which all data sets are well fitted, it is a useful exercise to experiment with different data weightings (or exclusion of some data sets). This provides important information about the robustness of our assessment. Not all stock assessments are sensitive to changes in data weighting (Breen et al. 2003; Savereide and Quinn 2004) but we can't know about any such sensitivity unless we investigate alternative weightings.

I offer brief comments on some earlier studies that consider data weighting. McAllister et al. (2001) considered just the weighting of abundance sets, in a setting different from that addressed here in that composition data were either not used (surplus production models) or were treated as known without error (Virtual Population Analysis). Gavaris and Ianelli (2002) identified data weighting as one of four generic statistical issues important in stock assessments and described two versions of two-stage weighting (one uses a special case of TA1.1 [see their Table 1]; in the other, the terms "extrinsic" and "intrinsic" [see their p. 257] apparently correspond to my "stage 1" and "stage 2"). Breen et al. (2003) estimated a parameter (their $\tilde{\sigma}$) that is the standard deviation of a component of error common to all data sets. This is an interesting approach that has little effect on point estimates of parameters, but has the merit of reducing the effect of changes in data weights on measures of the uncertainty of parameter estimates. Taylor et al. (2007), applying an approach to data weighting proposed by Stefánsson (2003), set weights for each data set according to how well it was fitted by the model when it was strongly up-weighted. This idea seems worth pursuing, but I think it would be much better if the objective function used proper likelihoods, rather than simple sums of squares, and of course Principle 1 must apply. Irwin et al. (2008) used concentrated likelihoods (i.e., weighting parameters were replaced by their maximum likelihood estimates), so that their data sets were essentially self-weighting, and then, as a sensitivity analysis, investigated the effect of sequentially up-weighting each data set by a factor of 10. This approach does not address the problem of correlations in composition data, nor does it give primacy to abundance data. Candy (2008) described a complicated stage-2 weighting method for composition data which involved treating the error in the model fit to these data as being the sum of two components: random error and systematic lack of fit. Though this characterization of the error seems sensible, I do not agree that the stage-2 weighting should include only the first component.

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Appendix A: Some methods of stage-2 weighting for composition data

In this appendix I provide equations for 10 methods of stage-2 weighting for composition data (Table A1) and describe their derivations.

McAllister and Ianelli (1997) presented a method of stage-2 weighting assuming a multinomial error structure. They assumed that the stage-2 sample size is the same for all years in a data set, and they took this sample size as the average of the N_{jy} calculated using TA1.1 (see eqs. (2.5) and (2.6) in their Appendix 2). Their approach is based on the fact that, with a multinomial distribution, $\mathrm{Var}(O_{jby} - E_{jby}) = \mathrm{Var}(O_{jby}) = E_{jby}(1 - E_{jby})/(w_j\tilde{N}_{jy})$, and also that $\mathrm{Var}(O_{jby} - E_{jby}) \approx (O_{jby} - E_{jby})^2$. Therefore, $E_{jby}(1 - E_{jby})/(w_j\tilde{N}_{jy}) \approx (O_{jby} - E_{jby})^2$. Equation TA1.1, which can be derived by summing this last equation over b and rearranging the terms, is a generalization of the method of McAllister and Ianelli (1997) in which the stage-2 sample size for each year is assumed to be a multiple of that for stage 1 (i.e., $N_{jy} = \tilde{N}_{jy}w_j$).

Method TA1.3 applies to the same situation as TA1.1 (i.e., weighting assumption T3.4) but its derivation is based on the assumption, that for each j, $\sum_{by}\frac{N_{jy}(O_{jby}-E_{jby})^2}{E_{jby}}$ has a χ^2 distribution with $m_{\mathrm{year},j}(m_{\mathrm{bin},j} - 1)$ degrees of freedom (this is the assumption underlying the usual χ^2 test used in the analysis of contingency tables) and so has expected value $m_{\mathrm{year},j}(m_{\mathrm{bin},j} - 1)$. Dunn and Hanchet (2009) used this same assumption to create method TA1.6 for the situation where weighting assumption T3.8 (i.e., $1/N_{jy} = 1/\tilde{N}_{jy} + 1/N_j$) is to be used. Note that eq. TA1.6 has no explicit solution for N_j (i.e., it must be solved numerically). However, in the special case where the initial sample sizes are the same for all years (i.e., $\tilde{N}_{jy} = \tilde{N}_j$ for all y) there is an explicit solution, which is method TA1.7.

The methods discussed so far use a multinomial error for the composition data. If, instead, we assume a lognormal error, with additive weighting assumption T3.6, it is possible to estimate the stage-2 weighting parameter, c_j, directly as a model parameter (i.e., c_j is chosen to minimize the objective function). This is method TA1.4, which was devised for CASAL (Bull et al. 2008).

In developing methods TA1.2 and TA1.5 I applied the same general approach to two specific situations. I will first describe the general approach, and then how it was applied in these two situations. The aim in this approach was to standardize the errors $(O_{jby} - E_{jby})$ so that they all have the same variance. That is, I wanted to find m quantities, X_{jby}, (which will be functions of the weighting parameter, w_j or c_j), so that the standardized error, $S_{jby} = (O_{jby} - E_{jby})/X_{jby}$, had constant variance, i.e., $\mathrm{Var}(S_{jby}) = k_j$, for all years y, and bins b. Here, I am thinking of the S_{jby} as being a set of m random variables whose distributions (determined by the assumptions of the multinomial or lognormal error model) all have mean 0 and variance k_j. When we do our stage-2 weighting, after running our stock assessment model, we can calculate the actual value of each of these standardized errors, and how that value changes as we change our weighting parameter. Our aim is to find the value of the weighting parameter that makes the variance of this set of m standardized errors, which I write as $\mathrm{Var}(S_{jby})$, equal to k_j. [Note the important distinction between $\mathrm{Var}(S_{jby})$, which is the variance of a random variable, and $\mathrm{Var}_{by}(S_{jby})$, which is the variance of a set of m numbers calculated from the model output].

Now I show how I applied this general approach to two specific situations. If we assume multinomial errors and $N_{jy} = w_j\tilde{N}_{jy}$ (i.e., weighting assumption T3.8) we can use

Table A1. Equations for some methods of stage-2 weighting of composition data, grouped by the weighting assumption (from Table 3) on which they are based, and whether they allow for substantial correlations (see text for explanations and sources).

Method	Weighting assumption	Equation	Allows for correlations?
TA1.1	T3.4	$w_j = (1/\tilde{N}_{jy}) \times \{[\sum_b E_{jby}(1 - E_{jby})]/[\sum_b (O_{jby} - E_{jby})^2]\}$	No
TA1.2	T3.4	$w_j = 1/\mathrm{Var}_{by}\{(O_{jby} - E_{jby})/[E_{jby}(1 - E_{jby})/\tilde{N}_{jby}]^{0.5}\}$	No
TA1.3	T3.4	$w_j = [m_{\mathrm{year},j}(m_{\mathrm{bin},j} - 1)]/[\sum_{by} \tilde{N}_{jy}(O_{jby} - E_{jby})^2/E_{jby}]$	No
TA1.4	T3.6	c_j estimated as model parameter	No
TA1.5	T3.6	$\mathrm{Var}_{by}\{(O_{jby} - E_{jby})/[E_{jby}(\tilde{c}^2_{jby} + c^2_j)^{0.5}]\} = 1$	No
TA1.6	T3.8	$\sum_{by}\{(O_{jby} - E_{jby})^2/[E_{jby}(1/\tilde{N}_{jy} + 1/N_j)]\} = m_{\mathrm{year},j}(m_{\mathrm{bin},j} - 1)$	No
TA1.7	T3.8[a]	$\frac{1}{N_j} = \{[\sum_{by}(O_{jby} - E_{jby})^2/E_{jby}]/[m_{\mathrm{year},j}(m_{\mathrm{bin},j} - 1)]\} - \frac{1}{\tilde{N}_j}$	No
TA1.8	T3.4	$w_j = 1/\mathrm{Var}_y[(\overline{O}_{jy} - \overline{E}_{jy})/(v_{jy}/\tilde{N}_{jy})^{0.5}]$	Yes
TA1.9	T3.8	$\mathrm{Var}_y\{(\overline{O}_{jy} - \overline{E}_{jy})/[v_{jy}(1/\tilde{N}_{jy} + 1/N_j)]^{0.5}\} = 1$	Yes
TA1.10	T3.6	$\mathrm{Var}_y[(\overline{O}_{jy} - \overline{E}_{jy})/(S_2^2 + S_1^2 S_3 - 2S_1S_4)^{0.5}] = 1^b$	Yes

Note: Var is the usual finite-sample variance function [for a sample $x_1,\ldots,x_n$, $\mathrm{Var}_k(x_k) = \sum_k (x_k - \overline{x})^2/(n-1)$, where $\overline{x}$ is the sample mean].

[a] With the additional assumption that $\tilde{N}_{jy} = \tilde{N}_j$ for all y.

[b] See text for definitions of S_1, S_2, S_3, and S_4.

the same equation as was used by McAllister and Ianelli (1997), viz. $\mathrm{Var}(O_{jby} - E_{jby}) = E_{jby}(1 - E_{jby})/(w_j\tilde{N}_{jy})$. This means that the errors can be standardized by setting $X_{jby} = [E_{jby}(1 - E_{jby})/\tilde{N}_{jby}]^{0.5}$, which makes $k_j = 1/w_j$, and leads to the equation for TA1.2. With lognormal errors, $\mathrm{Var}(O_{jby} - E_{jby}) = (E_{jby}c_{jby})^2$, so to standardize the errors we simply set $X_{jby} = E_{jby}c_{jby}$ and $k_j = 1$, which, together with the assumption $c^2_{jby} = \tilde{c}^2_{jby} + c^2_j$ (weighting assumption T3.6), produces method TA1.5. As with method TA1.6, this method requires numerical solution.

Methods allowing for correlations

None of the methods discussed so far has allowed for the possibility of substantial correlations within a data set. Methods TA1.1, TA1.2, TA1.4, and TA1.5 assume there are no correlations; the remaining methods allow only for the small negative correlations that are associated with the fact that all proportions must sum to 1 in each year.

To develop methods that allow for substantial correlations I used an approach similar to that described above for TA1.2 and TA1.5, except that, following Pennington and Vølstad (1994), the error to be standardized was $(\overline{O}_{jy} - \overline{E}_{jy})$, where $\overline{O}_{jy} = \sum_b (x_b O_{jby})$ and $\overline{E}_{jy}$ (defined similarly) are the observed and expected mean ages (or lengths), and x_b is the age (or length) associated with the bth bin. If our composition data set has a multinomial distribution then $\mathrm{Var}(\overline{O}_{jy} - \overline{E}_{jy}) = \mathrm{Var}(\overline{O}_{jy}) = v_{jy}/N_{jy}$, where $v_{jy} = \sum_b (x_b^2 E_{bjy}) - \overline{E}^2_{jy}$ is the variance of the expected age (or length) distribution. Therefore, with $N_{jy} = w_j\tilde{N}_{jy}$ (i.e., weighting assumption T3.4), $\mathrm{Var}(\overline{O}_{jy} - \overline{E}_{jy}) = v_{jy}/(w_j\tilde{N}_{jy})$ and we can standardize our errors by setting $X_{jy} = (v_{jy}/\tilde{N}_{jy})^{0.5}$, and $k_j = 1/w_j$. This produces stage-2 weighting method TA1.8, which can be solved explicitly for w_j. However, if $1/N_{jy} = 1/\tilde{N}_{jy} + 1/N_j$ (i.e., weighting assumption T3.8), we set $X_{jy} = [v_{jy}(1/\tilde{N}_{jy} + 1/N_j)]^{0.5}$ and $k_j = 1$, which leads to the equation for method TA1.9, which can be solved numerically for N_j.

When the composition data are assumed to have a lognormal error distribution, the calculations are a bit more complicated. Here, we need to impose the constraint (which is implicit with multinomial, but not lognormal, errors) that proportions sum to 1. Thus we treat $\overline{O}_{jy}$ as being equal to $\sum_b x_b O_{jby} / \sum_b x_b$, and calculate its variance using the standard approximation for the variance of a ratio of two random variables (eq. 10.17 of Stuart and Ord 1987), which produces $\mathrm{Var}(\overline{O}_{jy}) = S_2^2 + S_1^2 S_3 - 2S_1S_4$, where $S_1 = \sum_b x_b E^2_{jby}$, $S_2 = \sum_b (x_b c_{jby} E_{jby})^2$, $S_3 = \sum_b (c_{jby}E_{jby})^2$, and $S_4 = \sum_b x_b(c_{jby}E_{jby})^2$. Then we simply set $X_{jy} = \mathrm{Var}(\overline{O}_{jy})^{0.5}$ and $k_j = 1$, which leads to method TA1.10. Again, the equation for this method must be solved numerically (in this case we search for the value of c_j which makes the equation true, remembering that $c^2_{jby} = \tilde{c}^2_{jby} + c^2_j$).

Methods requiring numerical solutions

Finally, a word about what I mean above by "numerical solution" (and a reassurance that this solution is not difficult to achieve). Consider method TA1.5, where we are solving for the weighting parameter c_j. To solve this equation we first evaluate the left-hand side of the equation for $c_j = 0, 0.1, 0.2, \ldots$, continuing until a value greater than 1 is found. We might find, for example that for $c_j = 0, 0.1, 0.2$, and 0.3 the left-hand side of the equation has values 0.37, 0.56, 0.83, and 1.25, respectively, so that our solution lies between 0.2 and 0.3. Simple linear interpolation between the last two values produces the solution $c_j = 0.24$ $(= [0.2(1.25 - 1) + 0.3(1 - 0.83)]/(1.25 - 0.83))$.

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Table B1. Formulae for calculating normalized residuals for the example negative log-likelihoods of Table 2.

Table 2 likelihood	Formula
T2.1A	$(2\lambda_{ty})^{-1}(O_{ty} - E_{ty})$
T2.2	$(O_{ty} - E_{ty})/(c_{ty}E_{ty})$
T2.3	$(O_{ty} - E_{ty})/\sigma_{ty}$
T2.4A	$\{[\log(O_{ty}/E_{ty})]/\sigma_{ty}\} + 0.5\sigma_{ty}$
T2.5	$[\log(O_{ty}/E_{ty})]/\sigma_{ty}$

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Appendix B: Calculation of SDNRs

For each data point, O_{ty}, a normalized residual is a number that indicates how different that observation is from the model's expected value (E_{ty}), and that has been transformed so that its distribution is approximately normal, with mean 0 and SD 1 (assuming the likelihood for the data point is correct). To calculate the SDNR (standard deviation of the normalized residuals) for a data set, we first calculate the normalized residual for each data point (using formulae like those in Table B1) and then use the usual formula to calculate the standard deviation of these residuals. No formulae are given for the composition-data likelihoods because SDNRs are inappropriate for this type of data (because of correlations).

PERSPECTIVE / PERSPECTIVE

Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity [1]

Bryan D. Neff, Shawn R. Garner, and Trevor E. Pitcher

Abstract: Nearly 40% of commercial fisheries have now collapsed or are in serious decline. In response, governments have invested millions of dollars into artificial breeding programs, but many programs have failed to rehabilitate dwindling wild stocks. This failure may in part lie in the lack of knowledge about the genetic architecture of fitness: the genes and genotypes that are associated with individual performance. In this paper we discuss (*i*) artificial breeding programs, (*ii*) the genetic architecture of fitness, (*iii*) additive and nonadditive genetic effects on fitness, (*iv*) genetic diversity and evolvability, and (*v*) natural breeding and adaptation. We argue that most breeding programs do not maintain genetic adaptations and may consequently be ineffective at rehabilitating or enhancing wild populations. Moreover, there is no evidence that preserving genetic diversity as measured from neutral genetic markers increases fish performance or population viability outside of populations that experience strong inbreeding depression, and limited data that genetic diversity increases the potential for populations to adapt to changing environments. We suggest that artificial breeding programs should be used only as a last resort when populations face imminent extirpation and that such programs must shift the focus from solely preserving genetic diversity to preserving genetic adaptations.

Résumé : Presque 40 % des pêches commerciales se sont actuellement effondrées ou alors connaissent un important déclin. En réaction, les gouvernements ont investi des millions de dollars dans des programmes de reproduction artificielle; plusieurs de ces programmes n'ont pas réussi à rétablir les stocks en dépérissement. Cet échec peut en partie s'expliquer par un manque de connaissance de l'architecture génétique de la fitness : les gènes et les génotypes associés à la performance individuelle. Nous discutons ici (*i*) des programmes de reproduction artificielle, (*ii*) de l'architecture génétique de la fitness, (*iii*) des effets génétiques additifs et non additifs sur la fitness, (*iv*) de la diversité génétique et de l'évolubilité et (*v*) de la reproduction naturelle et de l'adaptation. Nous croyons que la plupart des programmes de reproduction ne préservent pas les adaptations génétiques et ainsi s'avèrent inefficaces pour rétablir ou renforcer les populations sauvages. De plus, il n'y a aucune indication que le maintien de la diversité génétique, mesurée par des marqueurs génétiques neutres, augmente la performance ou la viabilité de la population, à l'exception des populations qui connaissent une forte dépression consanguine; il y a des données restreintes qui indiquent que la diversité génétique augmente le potentiel des populations à s'adapter à des environnements changeants. Nous suggérons d'utiliser les programmes de reproduction artificielle seulement comme dernier recours lorsque les populations sont menacées d'extirpation imminente; ces programmes devraient être dédiés à la préservation des adaptations génétiques plutôt qu'à la seule conservation de la diversité génétique.

[Traduit par la Rédaction]

Introduction

Capture fisheries are a major contributor to the global economy and food supplies. Worldwide, capture fisheries harvest more than 90 million tonnes of fish each year, with a value of approximately US$90 billion (FAO 2009). These fisheries provide direct employment to more than 30 million people, the majority of which are small-scale commercial or subsistence fishers that operate in inland or coastal waters (FAO 2009). Including the contributions of capture fisheries and aquaculture, fish accounts for 15% of the total animal protein consumed by humans and close to 20% of animal

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protein in low income, food deficit countries (FAO 2009). Fishes are a particularly important food source because they are rich in *n*-3 fatty acids, which are associated with health benefits that include reduced risk of coronary death and improved early neurodevelopment (reviewed by Mozaffarian and Rimm 2006). Given the enormous value of the capture fisheries, protecting commercially harvested stocks is a key priority for agencies around the world that are responsible for resource management.

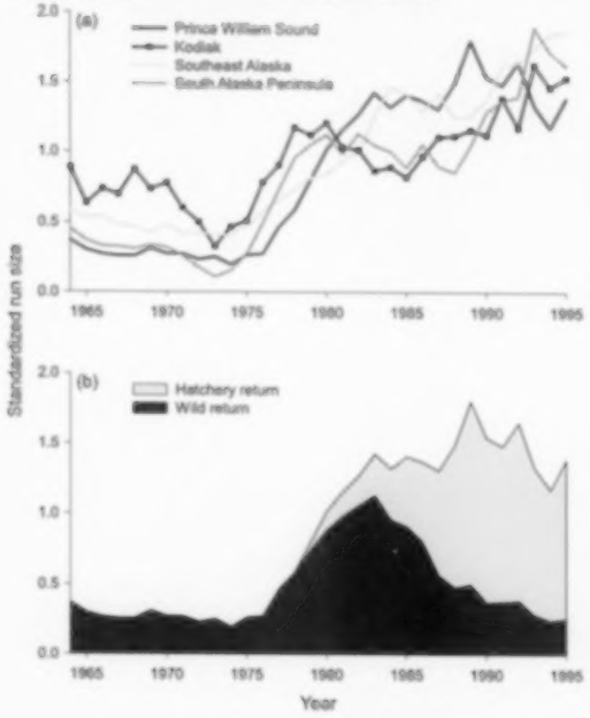
Despite the importance of capture fisheries, global yields appear to have reached a plateau, with many individual stocks in decline. For the last 20 years, the yields of capture fisheries have fluctuated in the range of 85–95 million tonnes per year, and when data from China are excluded, yields have shown a modest decline during this period (FAO 2009). Furthermore, over the last 20 years, catches of more than a quarter of all fished species fell below 10% of their previous levels (Worm et al. 2006), which includes high profile collapses such as the crash of the Atlantic cod (*Gadus morhua*) (Myers et al. 1997). Although factors such as habitat degradation may contribute to declines in fishery yields, a number of studies have identified overexploitation as the primary threat to fisheries sustainability (e.g., Jackson et al. 2001; Pauly et al. 2002; Myers and Worm 2003). Indeed, the Food and Agriculture Organization of the United Nations (FAO) has estimated that 28% of marine fisheries produce less than their maximum potential, owing to current or past overexploitation (FAO 2009; also see Hutchings et al. 2010). In contrast, only 2% of stocks are underexploited, with the remaining 70% of stocks either moderately or fully exploited (FAO 2009). Preserving existing fisheries and restoring depleted stocks are thus key objectives for conserving the global fisheries at what is likely the maximum yield of about 90 million tonnes annually.

Artificial breeding programs are common tools that are used in fishery management to augment or rehabilitate dwindling wild stocks (see Appendix A for definition of this and other terms used in this paper). These programs have the potential to increase stock sizes when populations are limited by juvenile recruitment and have been applied to a variety of fishery issues that include (Utter and Epifanio 2002): (*i*) to supplement declining populations and maintain genetic diversity so as to reduce the risk of local extinction; (*ii*) to preserve existing fisheries when anthropogenic activity, such as the construction of dams, degrades spawning habitat and disrupts natural ecological processes; and (*iii*) to enhance already healthy stocks of wild fish to provide additional opportunities for recreational or commercial fishers. Artificial breeding programs have been used to manage a wide range of fisheries such as Atlantic cod, flounder (*Paralichthys olivaceus*), and red sea bream (*Pagrus major*) (Masuda and Tsukamoto 1998; Svåsand et al. 2000). However, it is with salmonids that artificial breeding programs have been used most extensively as part of management strategies. Each year salmonid hatchery programs release more than 4.5 billion juvenile salmon into natural waters at a significant economic cost ranging up to about 100 million dollars (Hilborn 1998; Naish et al. 2008).

Despite the extensive use of artificial breeding programs for augmenting salmonid stocks, the effectiveness of the programs in meeting management goals is still poorly understood. Breeding program effectiveness remains poorly understood in part because the ubiquity of hatcheries on salmon bearing rivers makes it difficult to identify comparison populations without hatcheries and thus to conduct appropriately controlled scientific studies. For example, a recent evaluation of Pacific salmon (*Oncorhynchus* spp.) hatchery programs in the continental USA found that similar nonsupplemented populations could be identified for only 8 of the 22 hatcheries examined (Waples et al. 2007). Of those eight hatcheries, five (63%) supplemented populations had trends in abundance that were comparable to control populations, one (12%) supplemented population had lower abundance than its paired control population, and only two (25%) supplemented populations outperformed the paired control populations (Waples et al. 2007). A study of hatchery enhancement of pink salmon (*Oncorhynchus gorbuscha*) in Alaska similarly failed to provide clear evidence that artificial breeding programs were effective (Hilborn and Eggers 2000). Hatchery supplementation in the Prince William Sound and Kodiak Island areas of Alaska began in the mid-1970s, and by 1990, the annual releases in these areas exceeded a combined 600 million fry. Over this same period, salmon returns increased by a factor of about two, and generally the programs were touted as a success. However, Hilborn and Eggers (2000) also assessed the performance of pink salmon in two control sites comprising southeast Alaska and the South Alaska Peninsula, two other pink salmon producing regions in Alaska that neighbour Prince William Sound and Kodiak Island but that have never been subject to significant augmentation from artificial breeding programs. Comparing pink salmon abundance in the two control regions revealed that natural stocks increased at a similar rate to the artificially "enhanced" regions (Fig. 1*a*). Thus, the trends in abundance did not support a clear benefit of the artificial breeding programs. Moreover, when the contributions of wild and hatchery bred fish to the total run were compared in Prince William Sound and the Kodiak Island area, it became apparent that hatchery fish had largely replaced their wild counterparts in the most supplemented region, leading to a sharp decline in wild fish despite stable overall population size (Fig. 1*b*; Hilborn and Eggers 2000). These data suggest that artificial breeding programs for pink salmon in Alaska have largely led to replacement of wild fish with hatchery-bred fish as opposed to a clear enhancement of population size.

One area in which artificial breeding programs appear to have been successful is in the preservation of critically endangered populations. For example, aurora trout (*Salvelinus fontinalis timagamiensis*) were extirpated from the wild during the 1960s as a consequence of lake acidification in northern Ontario (Snucins et al. 1995). However, these fish escaped extinction, thanks to a hatchery program founded with nine individuals in 1958, which allowed the trout to persist in captivity and eventually be reintroduced to their native habitat (Snucins et al. 1995). The artificial breeding program for Chinook salmon (*Oncorhynchus tshawytscha*) in the Sooes River similarly appears to have been successful, as it was associated with a 10-fold increase in population size, from a low of less than 100 fish returning annually (Brannon et al. 1999; for additional examples see Brannon et al. 2004). Artificial breeding programs may thus be an important tool when populations are at risk of imminent extinction, but de-

Fig. 1. Run sizes of Alaskan pink salmon (*Oncorhynchus gorbuscha*) in relation to hatchery supplementation. (*a*) Run size of pink salmon in areas that received hatchery supplementation starting in 1975–1976 (Prince William Sound and Kodiak Island) and in areas that did not receive hatchery supplementation (southeast Alaska and the South Alaska Peninsula). (*b*) Contribution of hatchery and wild fish to the total returns of pink salmon in Prince William Sound. In both graphs, run sizes are presented as 5-year running averages that are scaled by the 1976–1985 average values in each area. The figure was redrawn from data presented in Hilborn and Eggers (2000) and Hilborn and Eggers (2001).



spite some notable successes, these programs have generally had low success at restoring stable populations in the absence of continued supplementation (Griffith et al. 1989; Fischer and Lindenmayer 2000).

Artificial breeding programs may also have unintended consequences that threaten the persistence of naturally occurring stocks. In salmonids, artificial breeding programs have been associated with negative effects on a number of important characteristics in the hatchery propagated fish. For example, hatchery-raised salmon show reduced foraging efficiency on live prey, reduced sensitivity to predation risk, and increased aggressiveness relative to wild individuals (e.g., Sundström and Johnsson 2001; Álvarez and Nicieza 2003; Sundström et al. 2003). These behavioural shortcomings may have considerable consequences for the fitness of hatchery fish. For example, the reproductive success of hatchery bred steelhead trout (*Oncorhynchus mykiss*) has been estimated to decline by about 40% for each generation of artificial breeding (Araki et al. 2007). Moreover, reproductive success was lower in wild born steelhead trout that had at least one hatchery-bred parent, which indicates a genetic basis to the reduced performance of hatchery fish (Araki et al. 2009). Artificially propagated fish may thus have serious negative effects on the genetic quality of wild fish when the two groups interbreed, which can threaten the genetic integrity and sustainability of wild populations (Ford 2002; Fraser 2008).

In this paper we review the approaches and objectives of artificial breeding programs with a focus on genetic aspects of fitness. We argue that current breeding programs are too focused on genetic diversity and thereby fail to acknowledge the complexities of the genetic architecture of fitness of wild populations. We detail these complexities and make broad, multi-tier recommendations to revamp the approach to management of wild fish populations, as well as make specific recommendations on how to conduct artificial breeding programs to maintain the genetic integrity and sustainability of wild populations. We begin by detailing the fertilization methodology used in current artificial breeding programs. We follow that section with an overview of the genetic architecture of fitness and the contributions of additive and nonadditive genetic effects to fitness and population viability. Finally, we discuss the role of natural mating in promoting and maintaining healthy gene pools.

Artificial breeding programs and fertilization methodology

Artificial breeding programs for fishes use either captive breeding or supportive breeding approaches. The breeding approach used depends on several factors, most notably the size and conservation status of the remaining wild population (Miller and Kapuscinski 2003; Kapuscinski and Miller 2007). When remaining populations are small and facing imminent extirpation or extinction, a captive breeding scheme is typically employed. Captive breeding brings into captivity a large proportion of the remaining individuals for the purpose of rearing subsequent generations for eventual re-release into the wild. In contrast, when remaining populations are more stable, but are either likely to become threatened in the near future or enhancement for increased harvest is desired, a supportive breeding scheme is a more common strategy. Supportive breeding is the practice of bringing into captivity only a small fraction of individuals from the wild for reproduction, for all or part of their life cycle, and then returning their offspring into their native habitat where they join their wild-produced counterparts (Ryman and Laikre 1991).

There are many genetic risks associated with the use of artificial breeding programs (reviewed in Miller and Kapuscinski 2003; Campton 2004; Fraser 2008). One risk that has attracted the most attention is the loss of genetic diversity (e.g., Hedrick 2001; Fiumera et al. 2004). Theoretical work indicates that this loss of genetic diversity stems from a reduction in effective population size mediated by an increase in variance in reproductive contribution among individuals (Ryman and Laikre 1991; Wang and Ryman 2001). Consequently, the most common breeding programs used today focus on the retention of genetic diversity through the maintenance of effective population size. These programs can be classified into four basic fertilization approaches: (*i*) mass mating; (*ii*) single-pair mating; (*iii*) nested mating; and (*iv*) factorial mating.

First, mass mating designs involve taking gametes from multiple members of each sex or multiple members of one sex and a single individual of the other sex, and mixing them together to achieve fertilization. For example, it was once common practice to employ a form of a mass mating design known as the "mixed-milt approach", where milt from several males was used simultaneously to fertilize the eggs of a single female. This protocol was initially popular because it was appropriate for broodstocks of all sizes, it was easy to accomplish, and hatchery managers believed it helped to ensure fertilization of the eggs in the event that one of the males' milt was either compromised during collection or functionally infertile. However, this practice has been eliminated from many programs because of the realization that this mating scheme can result in smaller effective population size owing to the differences in fertilization rates of the males, which arises from differences in the ability of males to succeed at sperm competition. For example, several studies on salmonid species, including Chinook salmon (Withler 1988; Withler and Beacham 1994), Atlantic salmon (*Salmo salar*) (Gage et al. 2004; Yeates et al. 2007), pink salmon (Gharrett and Shirley 1985), and coho salmon (*Oncorhynchus kisutch*) (T.E. Pitcher, D.D. Heath, and S. Al-Smoudi, unpublished data), have shown skewed paternity among competing males in mixed-milt fertilization trials. The differences in competitiveness has been directly attributed to variation in sperm density, velocity, and longevity among males (e.g., Hoysak and Liley 2001; Gage et al. 2004; Pitcher et al. 2009).

It is possible that sperm competition could increase offspring genetic quality if males that achieve higher fertilization success are also more effective in producing viable offspring (i.e., that there is heritable variation among males in their general viability or condition and that this variation is associated with that male's success in sperm competition — the so called "good-sperm hypothesis"; Yasui 1997). However, empirical support for the good-sperm hypothesis is limited (e.g., Hosken et al. 2003; Fisher et al. 2006; Simmons and Kotiaho 2007), and this hypothesis has yet to be tested in fishes. Thus, it is unclear whether sperm competition can improve genetic quality, yet it clearly results in unequal genetic contributions from males and lower effective population sizes than if the contributions were normalized. Indeed, Wedekind et al. (2007) attempted to experimentally assess the effect of sperm competition on effective population size in Alpine whitefish (*Coregonus zugensis*) and estimated that it could decrease the effective number of male breeders by up to 50%. Because of concerns about the negative effect that mass mating, and specifically sperm competition, has on effective population size, these kinds of spawning protocols have been removed from spawning guidelines for many hatcheries (e.g., Pacific salmon hatcheries in the Columbia River basin: Integrated Hatchery Operations Team 1995).

Second, single-pair mating designs, also known as a pairwise mating design, where one female and one male are used to produce offspring, is a popular technique in many hatcheries today because it gives each parent an equal opportunity to contribute genetically to the offspring gene pool owing to a lack of sperm competition. One of the major problems with this mating design is that if either parent is functionally infertile owing to, for example, poor sperm or egg quality, neither of the parents will contribute genetically to the pool of offspring. As such, this kind of mating design is typically recommended for larger broodstock programs in which the number of male and female adults available for spawning is sufficient to ensure a large effective population size despite the loss of a few of the crosses because of poor gamete quality (Campton 2004).

A variation of the single-pair mating design involves overlapping pairwise spawning schemes, where milt from a primary male is mixed with the eggs from one female, and the mixture is allowed to sit for a period of time before the milt from a second male is added in case the primary male has poor sperm quality. In a second spawning, the secondary male from the first mating becomes the primary male and the other male becomes the secondary male. This mating design assumes that the interval between the addition of sperm from the first and second male is sufficient to ensure that the first male has sperm precedence and will fertilize most of the eggs unless he is functionally infertile whereby the second male will garner all of the paternity. Recent work on Atlantic salmon has shown that just a two second delay between the release of the first and second males' milt can be sufficient to ensure that the first has sperm precedence and fertilizes most of the eggs (Yeates et al. 2007). However, breeding programs employing this overlapping scheme typically employ a delay of between 10 and 30 s (Withler and Beacham 1994).

Third, nested mating designs typically involve crossing a member of one sex with two or more members of the other sex. For example, one male may be crossed independently with each of three females or one female may be crossed with each of three males. This design is most commonly used when a single-pair mating scheme is not possible because of a strong skew in the sex ratio of parents. To compensate for skewed sex ratios, individuals from the less abundant sex are mated with two or more individuals of the more abundant sex. Importantly, unlike the mass mating scheme, nested mating schemes do not pool the milt but instead perform separate fertilization events with each additional mate. Consequently, sperm competition is eliminated and reproductive contributions from the broodstock are normalized within each sex. A drawback to the skewed sex ratio is that effective population size decreases dramatically with increases in the skew.

Fourth, more recently a full factorial mating design, which is also known as the matrix mating design, has been used (reviewed in Neff and Pitcher 2005; Busack and Knudsen 2007). In this design, males and females are crossed in all possible combinations. For example, Pitcher and Neff (2007) examined a variety of scenarios regarding supportive breeding for Chinook salmon using an 11 × 11 full factorial mating design. They split the eggs from each of 11 females into 11 batches of equal numbers and, for each female, fertilized each batch with milt from a different male. Thus, for a given female, 11 paternal half-sib families were generated. Assuming there are limited amounts of infertility, the underlying premise of the full factorial mating design is that each adult selected should have an equal opportunity and probability of producing an equal number of progeny with each potential mate, which in theory maximizes the number of genetic lineages produced. The full factorial mating design also has the advantage of facilitating the assessment of genetic and environmental components of phenotype and performance based on measurements taken of the offspring from the various families (e.g., Pitcher and Neff 2007; Wedekind et al. 2008). Despite these potential benefits, full factorial mating designs are not commonly used because they are logistically more difficult and expensive to conduct than the other three methods. To alleviate these problems, Withler and Beacham (1994) proposed a modified factorial mating design where eggs from *n* females are combined, mixed thoroughly, then split into *n* batches with each batch being fertilized by a different male. This modification reduces the number of fertilization events by a factor of *n*. However, it has the downside of potentially transmitting disease amongst eggs from different females and it negates the potential to examine genetic and environmental components of offspring phenotype, at least without reconstructing pedigrees using genetic markers. In addition, factorial mating designs in general have met some resistance by hatcheries because of a concern that the design can increase inbreeding depression because of the large numbers of half-sib families that are generated. However, such concerns are not supported by theoretical models, which show that inbreeding levels are instead reduced over multiple generations with either full or partial factorial mating designs (Engström et al. 1996; Dupont-Nivet et al. 2006).

Several attempts have been made to empirically and theoretically assess the efficacy of conducting single-paired matings versus partial or full factorial matings to maximize the effective number of breeders and ultimately the effective population size. Fiumera et al. (2004) used a factorial breeding design based on a modelling approach to implement an artificial breeding program for redhorse (*Moxostoma robustum*), an endangered North American cyprinid. They found that factorial mating can increase effective population size by nearly 20% and much of the benefit is achieved with as little as a series of 2 × 2 matings. In a second study, Dupont-Nivet et al. (2006) used a simulation approach to examine the utility of different mating designs to preserve genetic variability in populations undergoing selection. They found that a selection response was improved and inbreeding depression was reduced over multiple generations of a full factorial mating design and, again, that even just 2 × 2 crosses were superior to single-pair matings. Finally, Busack and Knudsen (2007) used simulations to examine the utility of four full factorial mating designs, 10 × 10, 20 × 20, 40 × 40, and 120 × 120, and three partial factorial mating designs, 2 × 2, 5 × 5, and 10 × 10, to maximize the effective number of breeders. They found that partial factorial mating in all but the smallest crosses achieved no less than half of the number of breeders and often a nearly equivalent number of breeders as the analogous full factorial design, and concluded that in practice there is often little need to consider full factorial designs. Partial factorial crosses thus provide artificial breeding programs with a logistically feasible breeding scheme that can maintain effective population size and maximize the number of genetic lineages.

Genetic architecture of fitness

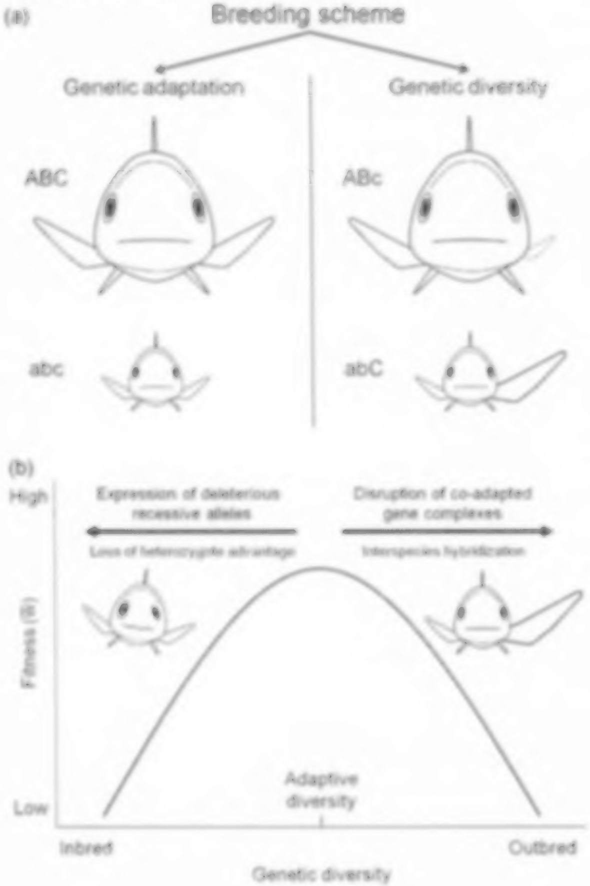
A major caveat in many artificial breeding programs is the sole focus on effective population size and the maintenance of genetic diversity. This approach ignores many of the complexities that underlie the genetic architecture of fitness and local adaptation. We argue that to maintain healthy wild populations, breeding programs must target the genes underlying fitness as opposed to genetic diversity per se, and to do so, we must have an understanding of the genetic architecture of fitness within populations.

The genetic architecture of fitness has two components that can be referred to as good genes and compatible genes (Neff and Pitcher 2005). A good gene is defined as a gene variant or allele that increases fitness independent of the architecture of the remaining genome, which, in diploid organisms, includes the homologue to the particular "good allele". Across the genome, good genes will show additive genetic variance. Thus, when variation exists among individuals in good genes quality, the population can respond to directional selection on fitness (for a review of additive genetic effects in salmonids see Carlson et al. 2008). A compatible gene is defined as an allele that increases fitness when in a specific genotype (i.e., when paired with a specific homologue (overdominance) or an allele at another gene locus (epistasis)). Across the genome, compatible genes show nonadditive genetic variance and the population does not respond to directional selection on this component of fitness. In the case of epistasis, compatible genes can take the form of a co-adapted gene complex, in which case an individual allele has either a positive or negative effect on fitness depending on the composition of the rest of the genome (Fig. 2*a*). In fishes, co-adapted gene complexes likely underlie complex traits such as foraging polymorphisms, which consist of a suite of morphological and behavioural characteristics that are adaptive only in specific combinations. For example, in threespined sticklebacks (*Gasterosteus aculeatus*), two morphologically distinct ecotypes are present in many lakes, with one adapted to feeding in open water habitat and the other to feeding in benthic habitat (Schluter 1993). Hybrid offspring of the two morphs are morphologically intermediate and have low foraging success and slow growth in either habitat (Schluter 1993, 1995). In conjunction with inbreeding depression, compatible gene effects can define an optimal level of diversity within individuals and populations (Fig. 2*b*; for examples, see Marshall and Spalton 2000; Neff 2004*a*).

The fitness contribution of an allele or genotype can be assessed by its contribution to an individual's lifetime reproductive success (LRS). Lifetime reproductive success is composed of both survivorship and breeding success: LRS = $\Sigma\, l_x \times m_x$, where l_x is the survivorship to age *x*, m_x is the breeding success as measured by the number of offspring that an individual produces at age *x*, and the summation is over an individual's lifetime (Stearns 1992). Individuals that have alleles or genotypes that are associated with either high survivorship or high breeding success will have higher fitness than individuals that have alleles or genotypes associated with low survivorship and breeding success. Because the effect that an allele or genotype has on fitness can vary across environments — referred to as a gene by environment interaction — fitness must be assessed in the context of the individuals' natural environment.

Studies of the genes of the major histocompatibility complex (MHC) have provided some of the best examples of both good and compatible gene effects (reviewed by Potts and Wakeland 1990; Apanius et al. 1997; Bernatchez and Landry 2003). The MHC is found in all jawed vertebrates

Fig. 2. Relationships among epistasis, genetic diversity, and fitness. (*a*) A hypothetical example of compatible gene effects arising from epistasis on fitness. For simplicity, genetic diversity is modeled for three haploid loci (A,B,C), which determined body size, right pectoral fin size, and left pectoral fin size, respectively. Each locus displays additive effects on morphology with the uppercase allele associated with large size and the lowercase allele associated with small size. In the breeding scheme on the left, genes are preserved in combinations that complement each other and maintain co-adapted gene complexes (high fitness). In contrast, the breeding scheme on the right preserves the same amount of genetic diversity, but because the genetic architecture of fitness is not considered, co-adapted gene complexes are disrupted and maladaptive phenotypes are produced (low fitness). Understanding the genetic architecture of fitness is thus critical in the design of breeding programs. (*b*) Expected relationship between genetic diversity and fitness. At low levels of genetic diversity, fitness is reduced by inbreeding depression, which arises from the expression of deleterious recessive alleles and the loss of heterozygote advantage. At high levels of genetic diversity, fitness is reduced by outbreeding depression, which arises from the disruption of co-adapted gene complexes and low viability of interspecies hybrids.


(a)
Breeding scheme
Genetic adaptation
Genetic diversity
ABC
ABc
abc
abC
(b)
High
Low
Expression of deleterious recessive alleles
Loss of heterozygote advantage
Disruption of co-adapted gene complexes
Interspecies hybridization
Fitness (W)
Adaptive diversity
Inbred
Outbred
Genetic diversity

and often includes a cluster of genes broadly classified into either the class I or class II types (in humans, the MHC is referred to as the HLA or human leukocyte antigen). The protein products of these genes are involved in immune response regulation. In many populations, the MHC is highly polymorphic and most individuals are heterozygous at the coding loci, presumably because those heterozygous individuals are able to present a wider range of foreign peptides to T-cells and thereby have a selective survivorship advantage over homozygous individuals (Klein and Figueroa 1986). In such cases, nonidentical homologues at either the class I or II genes can be considered compatible genes.

As an example, Arkush and colleagues (2002) used in vitro fertilization techniques with Chinook salmon to produce individuals that differed in their diversity at the MHC. Specifically, they were able to generate full-siblings that were either homozygous or heterozygous at the MHC class II set of genes. The researchers then exposed the families to infectious hematopoietic necrosis virus (IHNV). IHNV causes epizootics in salmonids and is considered to be one of the most important viral pathogens affecting these fish in North America (see Arkush et al. 2002). They found that for 7 of 10 families, survival was higher in the heterozygous siblings than the homozygous siblings, and they calculated the selection advantage of heterozygous individuals to be just under 10%. Their experimental approach was particularly powerful because by comparing full siblings carrying different MHC genotypes, the effects due to other segregating genes were minimized.

The MHC also provides an excellent example of good genes and serves to illustrate the distinction between good genes and compatible genes. Lohm et al. (2002) investigated interactions between specific MHC alleles and resistance to bacterial infection by *Aeromonas salmonicida* in Atlantic salmon (*Salmo salar*). Full-sibling broods were generated that contained individuals with different combinations of alleles. The researchers focused on two alleles, referred to as *e* and *j*. In the first experiment they generated siblings that were *e*/+, *j*/+ and *e*/*j*, where the + represents an allele other than *e* or *j*. Over an 18-day period post infection, they found that *j*/+ individuals had the lowest survivorship, while *e*/+ and *e*/*j* individuals had similar levels of survivorship. In a similar second experiment they generated siblings that were *e*/*e*, *j*/*j* and *e*/*j* and found that *j*/*j* individuals had the lowest survivorship, while *e*/*e* and *e*/*j* individuals had similar levels of survivorship. In this study, MHC heterozygosity was not important for increasing fitness, but possessing the *e* allele was important for increasing fitness. Indeed, Lohm and colleagues (2002) calculated the fitness advantage of possessing the *e* allele to be as high as 49%. Thus, in a population challenged predominately by *A. salmonicida*, the *e* allele would confer a fitness advantage and thereby represents a good gene. A similar result has been demonstrated in Alpine whitefish (Wedekind et al. 2004).

Additive and nonadditive genetic effects on fitness

Given that the genetic architecture of fitness has two components, it is important to understand the relative contributions of these components to variation in fitness in natural populations. Full factorial mating designs are one of the best ways to simultaneously measure the contributions of additive and nonadditive genetic variation to a trait (Lynch and Walsh 1998). Because full factorial designs mate a group of parents in all possible pairwise combinations and then compare the

Table 1. Summary of two-way analysis of variance (ANOVA) results from a full factorial breeding experiment in Chinook salmon.

Source	df	F	Variance ($\times 10^{-2}$)	Ttotal variance (%)	Genetic variance (%)	
Dam	10, 100	41.0	2.55	12.4	Maternal environmental	9.7
Sire	10, 100	9.0	0.56	2.7	Additive	10.8
Dam×Sire	100, 24 200	11.2	0.62	3.1	Nonadditive	12.4
Total	24 200		20.6			

Note: Additive genetic variance was calculated as four times the percent of total variance captured by the sire component, nonadditive genetic variance was calculated as four times the percent of total variance captured by the dam × sire component, and maternal environmental variance was calculated from the difference between the dam and sire component (Lynch and Walsh 1998). Genetic variance values are expressed as a percent of the total variance in survivorship. P values for all components were significant at $P < 0.001$. The results include source of variation in survivorship, degrees of freedom (df), F statistic, variance component, percentage of total variance, and genetic variance estimates. The data are from Pitcher and Neff (2007) and were reanalyzed following the methods in Puurtinen et al. (2009).

progeny from each family, variance associated with a trait can be partitioned into effects of the dam (maternal environmental effects and maternal additive genetic effects), the sire (paternal additive genetic effects), and the interaction between the dam and sire (nonadditive genetic effects). A recent review of 24 studies that used full factorial mating designs in a range of taxa found that the relative contribution of additive and nonadditive genetic effects on fitness-related traits were approximately equal, although the authors of the review were unable to calculate the absolute magnitudes from those studies (Puurtinen et al. 2009). Using the methods described by Puurtinen et al. (2009) and the data on Chinook salmon from Pitcher and Neff (2007) as one example, we found that additive and nonadditive genetic effects captured 10% and 12%, respectively, of the variance in early-life survivorship (Table 1). These studies collectively suggest that both additive and nonadditive genetic effects are important contributors to the genetic architecture of fitness.

Nonadditive genetic effects on fitness may arise from inbreeding depression, overdominance, or epistasis. Inbreeding depression occurs when the progeny of related parents have lower fitness than the progeny of unrelated parents. Inbreeding depression has been documented in a wide range of natural populations and generally arises as a consequence of small effective population sizes (Hedrick and Kalinowski 2000; Keller and Waller 2002). Inbreeding is thus a concern for many breeding programs because of its prevalence in threatened populations. Indeed, an examination of 170 threatened species found that genetic diversity was lower in the threatened species than in taxonomically related species that were not threatened for 77% (131) of comparisons. Specifically, heterozygosity at allozyme and microsatellite loci was about 35% lower in the threatened species than the nonthreatened species, albeit the fitness consequences of this reduced diversity were not measured (Spielman et al. 2004). In salmonids, inbreeding depression has been demonstrated for a number of fitness-related traits, but most studies have been done in captive environments using acute inbreeding between close relatives (Wang et al. 2002). Examining the consequences of inbreeding in wild populations that experience a gradual increase in the relatedness of breeding pairs over time, as might be the case for populations in decline, will be critical to determine the importance of inbreeding depression as a nonadditive genetic component of fitness in wild populations. Indeed, salmonids in particular may be somewhat buffered from the effects of inbreeding as compared with some other fishes because they have two copies of many genes (i.e., up to four alleles per individual) as a result of an ancestral genome duplication (Allendorf and Thorgaard 1984).

Nonadditive genetic effects can also influence fitness through overdominance. While there are several examples of strong overdominance effects at individual loci, such as the MHC described above, studies examining genome-wide levels of overdominance suggest that it has only a small effect on fitness. Such genome-wide effects have most commonly been assessed in large, outbred populations using heterozygosity–fitness correlations (reviewed by Coltman and Slate 2003; Hansson and Westerberg 2008; Chapman et al. 2009). A recent meta-analysis of over 600 reported correlation effect sizes from 73 studies showed only a small effect, with multilocus heterozygosity explaining less than 1% of the variance in life-history, morphological, and physiological traits (Chapman et al. 2009). These data might suggest that overdominance is a relatively insignificant component of fitness. However, the weak relationship probably arises in part because of the small number of microsatellite loci typically used to estimate heterozygosity–fitness correlations. Diversity at a small number of marker loci provides a reliable estimate of genome-wide heterozygosity only when there is strong identity disequilibrium between the marker loci and the rest of the genome, such as may be caused by inbreeding or admixture of different populations (Ljungqvist et al. 2010). Additionally, small numbers of marker loci are unlikely to capture strong overdominance effects at individual fitness-related loci, because recombination disassociates alleles at the marker loci from those of the fitness locus (Balloux et al. 2004). The studies examined by Chapman et al. (2009) may also fall on either side of an optimal level of genetic diversity (Fig. 2*b*) and thus capture both inbreeding depression and outbreeding depression, the effects of which may partially cancel out in the meta-analysis. Thus, although it is now recognized that a small number of neutral loci are unlikely to effectively estimate genome-wide levels of heterozygosity, the actually contribution of heterozygosity and overdominance to fitness, particularly at individual loci, is not yet well understood.

Nonadditive genetic effects may also arise from epistasis, which occurs when the effects of an allele are modified by an individual's genetic composition at other parts of the genome. For example, adaptive pigmentation differences in beach mice (*Peromyscus polionotus*) are determined by the genes of both the *melanocortin-1 receptor* (*Mc1r*) and *Agouti* *signaling protein* (*Agouti*), but *Mc1r* has an observable phenotypic effect only when individuals also possess a specific *Agouti* allele (Steiner et al. 2007). Epistasis may also arise from co-adapted gene complexes such as foraging polymorphisms as we have described above (Schluter 1993, 1995). In practice, it is statistically challenging to detect epistasis because the number of potential epistatic interactions between a group of genes is exponentially greater than the number of potential additive effects of those genes. Consequently, the importance of epistasis is not well understood outside of a few model systems (e.g., Tong et al. 2004).

Additive genetic variance, on the other hand, has been well studied, particularly within the salmonids. In those fishes, additive genetic variance has been documented as a component underlying a wide range of morphological, physiological, and life-history traits (for reviews see Garcia de Leaniz et al. 2007; Carlson and Seamons 2008). Additive genetic variance is often estimated from calculations of narrow sense heritability. For example, a review of 185 studies of salmonids found that estimates of the narrow sense heritability was highest for morphological traits (h^2 = 0.29), moderate for behavioral (h^2 = 0.20) and physiological traits (h^2 = 0.19), and lowest for life-history traits (h^2 = 0.16) (Carlson and Seamons 2008). Some caution is warranted when using heritability values to estimate additive genetic variance, because considerable additive genetic variation can exist even for traits with low heritability when there is large phenotypic variation. Consequently, low heritability of a trait does not necessarily translate into low additive genetic variance for that trait. Nevertheless, the studies on salmonids indicate that additive genetic variation can be an important component of fitness.

Genetic diversity and evolvability

What about the importance of maintaining genetic diversity for evolvability and future adaptation to a changing environment as opposed to for fitness in a current environment? Several researchers have postulated that populations with greater standing genetic diversity will be more likely to persist in changing environments, particularly those that result from anthropogenic activities such as climate change, than populations with lower standing genetic diversity (Lande and Shannon 1996; also see Petrie and Roberts 2007; for a review, see Colegrave and Collins 2008). For example, the oceans of the east and west coasts of Canada are predicted to increase in temperature over the next 50 years (IPCC 2007) and captive populations that maintain large amounts of genetic variation may have individuals with genotypes that are better suited for the anticipated warmer waters. While the idea may seem straight forward — it is more probable that a population with increased diversity will have an individual with a gene or gene variant that is better suited for some aspect of an altered environment than a population with decreased diversity — there is surprising little empirical evidence and none from fishes to support the claim.

Although we do not dispute that reduced genetic diversity can result in increased inbreeding depression, which in itself can reduce population viability and persistence (e.g., Markert et al. 2010), we emphasize here that there is limited data linking genetic diversity and the ability of a population to adapt and persist in a new environment (i.e., independent of the effects of inbreeding depression; for additional discussion of this point see Willi et al. 2006). To our knowledge, there is only a single experimental study to examine the role of genetic diversity and population adaptability to a novel environment in a sexually reproducing animal. Using laboratory populations of *Drosophila melanogaster*, Reed et al. (2003) tested the importance of genetic diversity and lineage on adaptability to a novel, stressful environment. They found that outbred populations showed a greater response in fitness, as measured by the number of progeny, than inbred populations when exposed to a sugarless growth medium for seven generations. Importantly, the effect was observed on the absolute increase in the number of progeny from the first to seventh generation, and thus their measure controls for differences in the starting number of progeny produced by the two types of populations. That is, although the outbred populations produced more offspring from the initiation of the experiment, those populations also showed a greater response and presumed adaptation to the sugarless diet through the seven generations of selection. Interestingly, the authors also found that populations that had been previously exposed to a different stressful environment (the presence of a toxin in the medium) were more likely to show positive fitness gains when exposed to the novel stressor. The authors also found strong lineage effects and lineage by environment interaction effects, which indicate a degree of unpredictability in the evolvability of populations based on the specific lineages that are used to found the population.

Other evidence for the importance of genetic diversity for population evolvability comes from correlational data. For example, Saccheri et al. (1998) studied a large metapopulation of butterflies (*Melitaea cinxia*) and found that the extinction risk increased significantly with decreasing heterozygosity, as measured using seven allozyme loci and one microsatellite locus, owing to reduced egg hatching rates, larval survival, and adult longevity. The data suggest that populations with increased genetic diversity are better able to persist, presumably because of continued adaptation to their environment. However, a later study showed that population growth was actually related to variation in just one of the allozyme loci. That gene locus coded for an enzyme involved in glucose metabolism and the resupply of energy to muscles during flight (Hanski and Saccheri 2006). Interestingly, the other six allozyme loci showed no evidence of overdominance, so it is unclear what drove the original pattern between population viability and multilocus heterozygosity. Regardless, there is remarkably scant data on the relationship between genetic diversity, population viability, and evolvability. Furthermore, studies of microbes indicate that evolvability stems from new mutations and not standing genetic variation (e.g., Lenski et al. 1991; Elena and Lenski 2003) and thereby suggest that maintaining genetic diversity is less important than increasing the rate of mutations. Of course microbes have vastly different biology from fish, and thus it is difficult to draw too much inference from the microbe studies. Yet other data shows both persistence and adaptation in populations that have experienced long-term bottlenecks and loss of genetic diversity (e.g., Lehman 1998). Clearly, more empirical studies are needed to understand the role of genetic variation in evolvability and its consequences for artificial breeding programs.

Natural mating and genetic adaptation

One of the major goals for most artificial breeding programs is to maintain genetic diversity by maximizing the effective population size, but reaching this goal often comes at the cost of reduced genetic fitness (Fraser 2008). Indeed, this objective has been criticized because it is not based on biological mechanisms found in natural mating systems (Tregenza and Wedell 2000; Pitcher and Neff 2007). Quinn (2005) points out that the fundamental problem with salmonid artificial breeding programs is that natural selection and sexual selection are essential for the continued viability of a population in the wild, yet no breeding design in a hatchery can possibly mimic these natural processes. For example, in salmonids, gravid females choose and prepare nest sites, males compete intensely for access to females, females spawn with a single or multiple males, which can promote sperm competition, and then those eggs are buried in the substrate until the fry emerge months later. It is interesting that natural and sexual selection almost invariably leads to nonrandom and nonuniform mating patterns and, as such, is in stark contrast to the approach used by artificial breeding programs.

In many species individuals do not mate randomly, but instead compete intensely for access to mates or are highly selective before accepting a potential mate (Andersson 1994). For example, male dominance in territorial contests is often an important determinant of breeding success, and, as a consequence, males of many species invest heavily into growth or other armaments that increase their success in such contests (Clutton-Brock 1982; Weckerly 1998). Alternatively, when members of one sex, typically females, are selective in which individuals they accept as mates, they can obtain direct benefits in resource-based mating systems (i.e., parental care or protection from predators) or indirect benefits (i.e., good or compatible genes) from their mate (review in Neff and Pitcher 2005). For example, females in some species are congruent in their mate choice for males that have an elaborate secondary sexual character such as a large ornament or bright colouration. Such congruent choice is typically for additive genetic benefits from good genes that the elaborate character "advertises" in the male (see Rowe and Houle 1996; Neff and Pitcher 2005). Alternatively, in other species, females are incongruent in their mating preferences and instead prefer different males. In a number of taxa, including salmonids and other fishes, this variation in preference has been linked to MHC diversity with females preferring MHC dissimilar males (e.g., Landry et al. 2001; Reusch et al. 2001; Garner et al. 2010). Increased MHC diversity in the offspring has been shown to increase pathogen resistance and survivorship of the offspring and thereby represents a nonadditive genetic benefit through compatible genes (e.g., Reusch et al. 2001).

To quantify the overall fitness benefits arising from mate choice, a number of studies have compared the offspring of individuals that mated with a preferred mate with the offspring of individuals that mated with a nonpreferred mate (Table 2). For example, female *Drosophila pseudoobscura* were allowed to select between two males in a mate choice arena and were then either mated to the preferred or nonpreferred male (Anderson et al. 2007). The number of offspring that survived to eclosion was about 20% higher for females that were paired with a preferred male than for females paired with a nonpreferred male. Similar results were found when males were instead allowed to select between pairs of females. Another study in guppies (*Poecilia reticulata*), which used a similar design, found that preferred males sired offspring that were about 3% larger at birth than the offspring of nonpreferred males (von Ompteda 2003). Larger body size, especially early in life, can have large effects on survivorship in fish (Miller et al. 1988; Neff 2004*b*). No similar study, however, has been conducted on salmon. Nevertheless, across a range of taxa, sexual selection has been linked to a 36% median increase in fitness-related traits in the offspring (Table 2; but also see Møller and Alatalo 1999). Furthermore, mate choice can contribute to reproductive isolation between ecologically distinct groups of fish and thus helps preserve local adaptations to unique habitats (Hendry et al. 2000; Rundle et al. 2000).

Although sexual selection is often studied to understand patterns of natural diversity, there is an increasing awareness that sexual selection may be relevant to artificial breeding programs and managing captive populations (Wedekind 2002; Pitcher and Neff 2007). Artificially propagated animals typically experience little or no sexual selection, and when breeding pairs are chosen by managers, mate choice and male–male competition are excluded entirely. Many artificial breeding programs aim to maximize genetic diversity by ensuring that all individuals reproduce, which contrasts with natural breeding systems in which variance in reproductive success among individuals is typically high and that variance is often associated with the fitness of the offspring (Wedekind 2002; Quinn 2005). By allowing low-quality individuals to reproduce, or by mating individuals that are not genetically compatible, artificial breeding programs may actually facilitate the accumulation of maladaptive alleles and genotypes that might otherwise be purged by sexual selection (Quader 2005).

Only a few studies in fishes have critically evaluated the performance of offspring produced by natural mating with those produced by artificial mating through their entire life cycle. Consuegra and Garcia de Leaniz (2008) examined the linkage between mate choice, MHC variation, and offspring fitness in a natural population of Atlantic salmon. The authors compared MHC diversity and internal parasite prevalence among anadromous Atlantic salmon returning to rivers to spawn that had originated from natural spawning, where parents were allowed to mate freely, or artificial crosses. They found that offspring from artificially bred salmon had higher parasite loads and were four times more likely to be infected than salmon originated from parents that were allowed to mate freely. The authors attributed this difference to the fact that the naturally bred fish were more MHC dissimilar than would be expected by chance. In a second study, Agbali et al. (2010) used the Chinese rose bitterling (*Rhodeus ocellatus*) to examine the additive and nonadditive genetic benefits of mate choice. The authors first used a factorial breeding design and tracked the offspring through to sexual maturity and found a significant nonadditive genetic component to the genetic architecture of fitness that accounted for 36% of the variance in survival and 30% of the variance in growth rate. They then examined female mate choice and compared the performance of offspring from matings with preferred and nonpreferred males. Female mating preferences captured a significant portion of the nonadditive

Table 2. Experimental demonstrations of the benefits associated with natural mating.

Method of comparison	Species	Fitness measure	Effect size (%)	Reference
Sexual selection: female choice				
Preferred vs. nonpreferred	House mice (*Mus musculus*)	Offspring survival in field enclosures (60 days)	72%	Drickamer et al. 2000
		Dominance of male offspring	133%	Drickamer et al. 2003
	Guppy (*Poecilia reticulata*)	Offspring size at birth	2.7%	von Ompteda 2003
		Offspring condition and critical swim speed	NS	Nicoletto 1995
	Pacific blue-eye (*Pseudomugil signifer*)	Offspring hatching success	547%	Wong 2004
	Deep-snouted pipefish (*Syngnathus typhle*)	Offspring survival following predator exposure	57%	Sandvik et al. 2000
		Offspring growth rate	36%	Sandvik et al. 2000
	Drosophila pseudoobscura	Number of offspring surviving to eclosion	20%	Anderson et al. 2007
Choice vs. random mating	*Hyalella* amphipods	Mating success of male offspring	59%	Cothran 2008
Sexual selection: male choice				
Preferred vs. nonpreferred	House mice (*Mus musculus*)	Offspring nest quality in field enclosures	23%	Gowaty et al. 2003
		Dominance of male offspring	50%	Drickamer et al. 2003
	Deep-snouted pipefish (*Syngnathus typhle*)	Offspring survival following predator exposure	42%	Sandvik et al. 2000
	Drosophila pseudoobscura	Number of offspring surviving to eclosion	17%	Anderson et al. 2007
Sexual selection: male competition				
Dominant vs. subordinate	Bank voles (*Myodes glareolus*)	Offspring survival to weaning	40%	Kruczek and Zatorska 2008
	Pacific blue-eye (*Pseudomugil signifer*)	Offspring hatching success	NS	Wong 2004
	Brown trout (*Salmo trutta*)	Offspring hatching success and survival	NS	Jacob et al. 2007
	Rose bitterling (*Rhodeus ocellatus*)	Offspring survival	NS	Casalini et al. 2009

Note: Effect size was calculated as high/low – 1 and is expressed as a percentage. The effect of mate choice was assessed by comparing offspring produced by preferred and nonpreferred individuals, whereas the effect of competition for mates was assessed by comparing offspring produced by dominant and subordinate individuals. Pacific blue-eye breeding system is characterized by male-only parental care; female choice is presumably for parental care. Included are the mechanisms of sexual selection (mate choice or intrasexual competition), method of comparison, species, fitness measure, effect size, and the source reference.

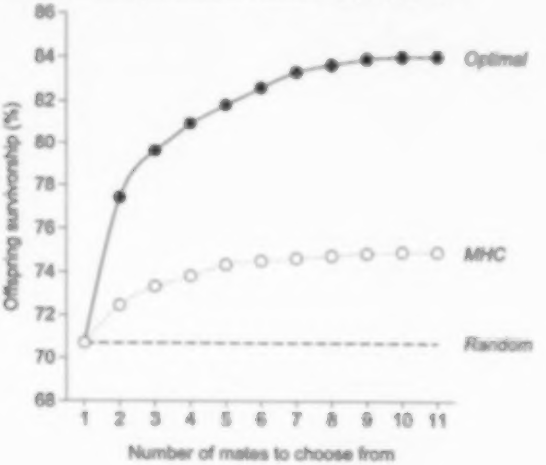
effects on fitness and offspring from preferred matings outperformed those from matings with nonpreferred males. Agbali and colleagues (2010) also implicated the MHC as part of the nonadditive genetic effect because they found that females preferred males that were dissimilar from them at the MHC.

The potential for mate choice to make an impact on the genetic quality of offspring produced from artificial breeding programs has also been assessed using a modelling approach. These models typically use a full factorial breeding design to detail the components of the genetic architecture of fitness and then assess the potential increase in offspring genetic quality from optimal mating (i.e., maximize familial fitness for each female), optimal mating based on a single candidate fitness locus such as the MHC, and random mating. For example, Pitcher and Neff (2007) modelled the value of incorporating genetic quality into supportive breeding programs for Chinook salmon through increases in offspring survivorship. Their model revealed that females that selected optimal males would increase their offspring survivorship by 19% during just the endogenous feeding period as compared with random mating (Fig. 3). Additionally, even if optimal mating was based only on a single fitness locus, the MHC class II, offspring fitness could be increased by 6% (also see Pitcher and Neff 2006). These modelling studies, in conjunction with empirical data showing that females do discriminate among males based on genetic quality, show the potential for incorporating natural mating into supportive breeding programs.

Recommendations for the management of wild fish populations

In the text below, we make hierarchical recommendations for the effective management and conservation of wild fish populations. We believe that each subsequent recommendation will be less effective at maintaining healthy wild popula-

Fig. 3. Model demonstrating the potential increase in offspring survivorship from mate choice in Chinook salmon (*Oncorhynchus tshawytscha*). The Random line represents the expected (average) offspring survivorship through to the end of the endogenous feeding period for females randomly mated to a single male. The MHC line and data points represent the potential benefit to selecting among up to 11 males optimally based on MHC genotype. The Optimal line and data points represent the potential benefit to selecting among up to 11 males optimally based on overall survivorship. The figure was redrawn from data presented in Pitcher and Neff (2007).



tions, but may be required when competing demands for ecosystem services are considered. In all cases, these recommendations should be implemented with the target of preserving existing populations in their native habitat to avoid the potential loss of local adaptations.

1. Rehabilitate and maintain healthy habitat and ecological function. Quinn (2005, p. 1491) wrote about salmon conservation, "No hatchery manager, regardless of the guidelines that he or she is given, can reproduce the patterns of breeding and selection that would occur in the stream." We share the concern of Quinn and others (e.g., Meffe 1992; Waples et al. 2007; Fraser 2008) that anthropogenic attempts to breed fish via artificial breeding programs are destined to produce individuals that are not well adapted to their local environments. Maintaining healthy habitats and ecological processes (e.g., sexual and natural selection) is the only effective approach to ensure the persistence of wild populations. Sexual selection can have enormous effects on mating patterns and can promote genetic quality in offspring. Competition for mating opportunities can improve genetic quality by preventing individuals that have genes associated with poor condition from reproducing, and facilitating mate choice can promote both good genes and compatible gene combinations. In systems where viable spawning habitat remains, the goal of the management program should be to ensure that a large and representative group of mature fish reach the breeding grounds. Constructing artificial breeding habitats may likewise facilitate sexual selection and its associated benefits in areas where natural breeding habitats are limited. Such artificial habitats, however, should retain as much of the natural environment as possible, including, for example, exposure to water from the native stream including the natural pathogen community, natural food and prey items for the fry once they emerge, and some level of predation.
2. Incorporate natural ecological processes into artificial breeding programs. When augmented breeding is required, for example, because of the lack of healthy habitats or very low population sizes, incorporate as many aspects of natural ecological processes as possible. Sexual selection could be incorporated into breeding programs by facilitating mate choice and male–male competition. For example, mating preferences might be incorporated into artificial breeding schemes by allowing females to select from multiple males in a choice arena, as is routinely done in mating system research. The female and selected male could then be spawned following conventional hatchery procedures. Seminatural spawning channels have been used to breed salmon for scientific and sometimes commercial interests and can facilitate both male–male competition and mate choice. Alternatively, anthropogenic mate selection could target phenotypic traits including behaviours that are known to be subject to sexual selection with the premise that those traits are associated with genetic aspects of quality. Features of natural selection such as disease challenges and predation should be incorporated to some degree to minimize or counter selection imposed by the artificial hatchery environment and to promote genes associated with local adaptation to the natural environment.
3. Use a full or partial factorial breeding design in artificial breeding programs. When spawning habitat is compromised and seminatural habitat is inaccessible or logistically infeasible, implementing a full or partial factorial breeding design can maximize the number of genetic lineages produced and provide a wide target for natural and sexual selection to operate. To that end, the families should be maintained in the artificial environment for the minimal amount of time, and consideration of equalizing family sizes immediately prior to release into the natural environment should be considered. Equalization may help to reduce unintended selection imposed within the artificial environment. Additionally, when known, aspects of the genetic architecture of fitness could be incorporated into the breeding program. Additive genetic effects (good genes) sometimes can be identified phenotypically via condition-dependent traits. The advent of next-generation sequencing enables a wealth of genetic data to be generated even in nonmodel species, which considerably increases the capacity to identify genetic variation that contributes to adaptation (Stapley et al. 2010).

In all the cases noted above, broodstock should always come from the population targeted for management. When the target population has been extirpated, broodstock should come from another population that has a similar genetic architecture of fitness or, given that the architecture generally is unknown, from an ecologically similar population.

Conclusions

We have argued that there is little scientific evidence that artificial breeding programs meet their objective of rehabilitating or enhancing wild populations. We feel that the failure of these programs stems in part from a lack of appreciation for the complexity of the genetic architecture of fitness. Outside of small populations that suffer from strong inbreeding depression, programs that focus solely on maintaining genetic diversity may be less effective than those that also include consideration of the genetic architecture of fitness. Broad generalizations about the genetic architecture of fitness, such as maintaining genetic diversity via indices of multilocus heterozygosity, are too simplistic to be effective and should be abandoned. The evidence from natural populations indicates that outside of inbreeding depression in small populations, multilocus heterozygosity does not contribute to fitness. Even temporal monitoring of neutral diversity at a small number of loci is unlikely to provide insight into population demography that is not already available from hatchery breeding records and natural abundance surveys. Maintaining genetic diversity to allow populations to evolve in response to changing environments is theoretically plausible, but it is not yet supported empirically. More research is needed in this area before any meaningful recommendation can be made about the importance of genetic diversity for the evolvability of populations and future adaptation in fishes and how best to measure such diversity to maximize evolvability. Ultimately, artificial breeding programs should only be considered as a short-term solution to the management of populations that are in imminent peril of extirpation. Effective management otherwise should take a broader ecosystem approach and focus on maintaining healthy habitats and natural ecological processes. More generally, it has become apparent that the world fisheries are fully taxed and cannot meet any further increase in global demand for fish products. Such demand must instead be diverted to alternative sources including aquaculture. Indeed, of the four major sources of animal protein for human consumption, comprising chicken, pork, beef, and fish, only fish are not yet domesticated and widely farmed.

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Appendix A. Glossary of terms

Artificial breeding programs — the planned breeding of organisms in captivity for the purpose of conservation or production.

Captive breeding — the bringing into captivity a large proportion of a critically endangered population to rear subsequent generations for eventual re-release into the wild.

Compatible genes — alleles whose effects on fitness depend on the genetic architecture at the rest of the genome and thereby show nonadditive effects.

Ecosystem services — the total direct (i.e., harvest opportunities) and indirect benefits (i.e., biodiversity conservation) provided by an ecosystem.

Epistasis — genes whose effects are modified by the genotype at one or more other loci.

Evolvability — the ability of a population to exploit existing genetic variation to respond to natural selection. Broader definitions also include the ability of the population to generate genetic variation, albeit in this review we focus on the first part of the definition.

Fitness — the number of copies of its genes that an individual contributes to the next generation. Typically measured as lifetime reproductive success.

Gene pool — all of the alleles present in a population.

Genetic architecture of fitness — the underlying genetic basis of fitness or fitness-related traits.

Good genes — alleles that increase fitness independent of an individual's genetic architecture at the rest of the genome and thereby show additive effects.

Identity disequilibrium — a nonrandom association of alleles at two or more loci. Not necessarily caused by physical linkage of loci on the same chromosome, but can for example arise when inbreeding leads to loss of heterozygosity at both marker loci as well as the rest of the genome.

Inbreeding depression — negative effects of inbreeding on fitness that typically arises because inbreeding exposes deleterious recessive alleles to selection or because of reduced heterozygosity and the loss of benefits from overdominance.

Local adaptation — alleles that increase fitness in one location, but not in other locations within the habitable range of the species.

Mate choice — nonrandom mating arising from a preference by one sex (usually females) for specific characteristics when selecting mates.

Narrow-sense heritability — proportion of the total phenotypic variation within a population that is explained by additive genetic variation.

Natural selection — a difference in survival or reproductive success arising from phenotypic differences among individuals. When phenotypic differences are heritable, these fitness differences can lead to evolution.

Next-generation sequencing — simultaneous sequencing of multiple target DNA sequences providing upwards of millions of sequence reads in a single run.

Overdominance — a heterozygote advantage in which individuals that are heterozygous at a locus have higher fitness than individuals who are homozygous for either of the alleles present in the heterozygous individual.

Secondary sexual character — a sexually dimorphic characteristic that is not part of the reproductive system. Typically involved in sexual selection through effects on mate choice or competition for mates.

Sexual selection — selection arising from differences in mating success among individuals within a population. Typically arises either from mate choice or from competition within a sex for mating opportunities.

Sperm competition — competition between the sperm of two or more males to fertilize an ovum.

Standing genetic variation — the presence of multiple alleles at a locus within a population.

Supportive breeding — bringing into captivity a small fraction of individuals from the wild for reproduction and then returning their offspring into their native habitat.

CORRIGENDUM / RECTIFICATIF

Corrigendum: Historical abundance of Puget Sound steelhead, *Oncorhynchus mykiss*, estimated from catch record data

N. Gayeski, B. McMillan, and P. Trotter

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